Contribution to the biosystematics of *Celtis* L. (Celtidaceae) with special emphasis on the African species

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This study was carried out at the NHN-Wageningen, Biosystematics Group,
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To my parents
my wife (Forogh)
and my children (Mohammad Reza, Mobina)

Contents

Chapter 1

GENERAL INTRODUCTION

Summary

The research questions of the project are introduced. In this thesis, the results are presented of biosystematic studies in *Celtis*, particularly African *Celtis*, the type genus of Celtidaceae, formerly Ulmaceae-Celtidoideae (Elias 1970; Grudzinskaya 1967; Judd et al. 1994; Omori & Terabayashi 1991, 1993; Ueda et al. 1997; Song et al. 2001). The African species of *Celtis* have been revised. We introduce the history of the Ulmaceae family (morphology and phylogeny).

1.1 Phylogeny

During the last decade, our knowledge and understanding of phylogenetic relationships within the Angiosperm has improved, this has been accomplished largely based on various studies (e.g. Chase et al. 1993; Chase and Cox 1998; Soltis et al. 1998; Hilu et al. 2003). The classifications of the Angiosperm phylogeny group (APG 1998; APG II 2003) have been on the basis of these molecular and phylogeny studies, leading to the recognition of a series of monophyletic orders and families. Despite of advances in understanding phylogenetic patterns, there is a need for more studies addressing the phylogeny and relationships between morphology and phylogeny based on DNA sequences (Endress et al. 2000; Nandi et al. 1998; Doyle & Endress 2000; Zanis et al. 2003; Walter et al. 2004).

What are the tools available today? Phylogenetic methods and data used: DNA sequences, cpDNA, MP, ML, Bayes. There are large advantages of using molecular data in phylogeny, the main ones are the large number and reliability of characters, or data power (e.g. Chase 1993). Moreover, homology assessment is easier for DNA sequence data than for morphology in angiosperm plants.

Recent molecular-phylogenetic research has shown that relationships of the Urticales are different from what was based on morphological characters; here we briefly introduce some part of the phylogeny of Ulmaceae. Molecular data show the place of Urticalean families within a well-defined and supported Rosales (sensu APG 1998; including Barbeyaceae, Dirachmaceae, Eleagnaceae, Ramnaceae, and Rosaceae (Chase et al. 1993; Gunter, Kochert, & Giannasi 1994; Soltis et al. 1997; Qiu et al. 1998) and also shows that *Celtis, Humulus, Trema,* and *Boehmeria* in an Urticalean clade with *Morus* and *Ficus* and Urticalean clade is placed in their Rosid I clade, closely related to Rhamnaceae and Rosaceae (Chase et al. 1993). Molecular studies within Urticalean rosids included a restriction site mapping analysis of plastid DNA that indicated Ulmaceae were sister to the rest (Wiegrefe et al. 1998; Sytsma & Guries 1998). A preliminary *rbcL* analysis of the Ulmaceae and Celtidaceae (11 genera) and four genera representative of other Urticalean families provided strong support for a monophyletic Ulmaceae sister to a broadly paraphyletic Celtidaceae including Urticaceae, Moraceae and Cannabaceae (Ueda et al. 1997).

The three-gene analysis of Soltis et al. (2000) also provided strong support for the separation of Ulmaceae and Celtidaceae. A small-scale *matk* analysis of Celtidaceae (5 genera of Celtidaceae and 8 other genera of Urticalean rosids) placed Cannabaceae solidly within a portion of the Celtidaceae (Song et al. 2001).

Table 1.1. Main history of Ulmaceae Mirbel.

Author	**Date**	**Family**	**Genera**
Mirbel	1815	Ulmaceae Mirb. s.l.	*Ulmus, Holoptelea, Phyllostylon, Planera, Hemiptelea, Zelkova, Lozanella, Ampelocera, Celtis, Pteroceltis, Trema, Parasponia, Aphanthe, Gironniera, Chaetachme, Plagioceltis, Chaetoptelea, Barbeya. Mirandaceltis*
Link	1831	Ulmaceae Mirb. s.s.	*Ulmus, Holoptelea, Phyloptelea, Phyllostylon, Planera, Hemiptelea, Zelkova.*
		Celtidaceae Link	*Lozanella, Ampelocera, Celtis, Pteroceltis, Trema, Parasponia, Aphananthe, Gironniera, Chaetachme*
Engler	1907	Ulmoideae	*Ulmus, Holoptelea, Phyloptelea, Phyllostylon, Planerar, Hemiptelea, Zelkova.*
		Celtidoideae	*Lozanella, Ampelocera, Celtis, Pteroceltis, Trema, Parasponia, Aphanathe, Gironniera, Chaetachme, Mirandaceltis*
Grudzinskaya	1965	Ulmaceae Mirb. s.s.	*Ulmus, Holoptelea, Hemiptelea, Zelkova, Planera, Phyllostylon.*
		Celtidaceae Link	*Celtis, Pteroceltis, Trema, Parasponia, Lozanella, Aphananthe, Gironniera, Chaetachme, Ampelocera*
Hutchinson	1967	Ulmeae	*Ulmus, Phyllostylon, Planera, Holoptelea,*
		Celteae	*Celtis, Mirandaceltis, Pteroceltis, Ampelocera, Zelkova, Hemiptelea, Trema, Parasponia, Aphananthe, Gironniera, Chaetachme, Lozanella*
Sweitzer Soepadmo Ulloa	1971 1977 1995	Ulmoideae	*Ulmus, Holoptelea, Phyllostylon, Planera, Hemiptelea, Zelkova,*
		Celtidoideae	*Lozanella, Ampelocera, Celtis, Pteroceltis, Trema, Parasponia, Aphanathe, Gironniera, Chaetachme*

Ulmaceae and Celtidaceae are separate families (Sytsma et al. 2002) while Cannabaceae and Celtidaceae should be merged. The origin of Cannabaceae within a clade of Celtidaceae is supported by ultrastructure, chromosome number, and cpDNA restriction site (Wiegrefe et al. 1998) and *matk* data (Song et al. 2001) as well as with these *rbcL, trnL-F,* and *ndhF* sequence data. All the analyses of Sytsma et al. (2002) are based on *rbcL*, *trnL-F* and *ndhF*. *Gironniera* is sister to a clade comprising *Celtis*, *Chaetachme*, *Parasponia*, *Pteroceltis* and *Trema*, but these relationships are not well supported (Song et al. 2001).

1.2 Morphology

The family Ulmaceae Mirbel (sensu lato) consists of 15-19 genera and 150-200 species, depending on the authority quoted (Table 1.1). Link (1831) was of the opinion that the Ulmaceae had to be split into separate families: the Ulmaceae (*Ulmus* and related genera) and the Celtidaceae (*Celtis* and related genera) (Table 1.2). This proposal has not been generally accepted since that time.

The Ulmaceae (Engler 1907) are divided in two subfamilies (Celtidoideae), and (Ulmoideae) (Table 1.1). Hutchinson (1976) divided the Ulmaceae genera in two tribes, Ulmeae and Celteae, according to the fruit type (fleshy fruits versus dry samara) and the major dispute appears to lie within the family. As Engler (1907) and Sweitzer (1971) indicated in their taxonomic reviews and anatomical studies of the family, the majority of morphological authorities considered the Ulmaceae

Table 1.2. Main characters of Celtidaceae Link.

Character	**Description**
Habit	trees, shrubs, monoecious
Genera/species	9 genera, 150 spp. *Celtis, Pteroceltis, Parasponia, Lozanella, Ampelocera, Trema, Aphananthe, Gironniera, Chaetachme.*
Leaves	simple, alternate, opposite, venation between pinnate and palmate,
Inflorescences	axillary, solitary, in cymes, short panicles
Flowers	sepals 4-5(6), stamens 4-6 opposite, carpels 2, hermaphrodite and male flowers
Pollen grains	2-3-porate
Fruits	drupe, folded embryo
Pollination	wind pollination, insect pollination
Wood anatomy	homocellular rays, heterocellar rays, ring and diffuse porous
Chromosome number	X=10
Usage	economic plants, timber, ornamental trees
Distribution	mainly Africa, Asia, South America

to consist of two subfamilies; the Ulmoideae and the Celtidoideae (Engler 1907; Cronquist 1981 1988; Sweitzer 1971). Each subfamily consists of a core of five or six genera, which characterize the subfamily, while the remaining six-seven genera are variously shifted from one group to another (this thesis, chapters 1 & 6).The two subfamilies are based on evidence from floral anatomy (Chernik 1975, 1981), fruit morphology (Chernik 1980), seed coat anatomy (Chernik 1982), embryology, wood anatomy (Sweitzer 1971), pollen morphology (Zavada 1983; Takahashi 1989), leaf venation (Terabayashi 1991), and flavonoid chemistry (Bate-Smith & Richens 1973; Giannasi 1978). The Ulmoideae with their slightly larger hermaphroditic flowers and pollen, spiral perianth and stamen traces are considered to be more primitive than the Celtidoideae (Cronquist 1981, Leroy 1952; Hutchinson 1958; Soepadmo 1977). Advanced characters in the Celtidoideae include smaller flowers; fewer stamens, whorled perianth, and the absence of any vestigial stamen, permitting recognition of two sub-families. Many members of the Celtidoideae have a greater affinity to the Moraceae than to other Ulmaceae (Grudzinskaya 1967; Chernik 1975, 1980, 1981, 1982; Takaso & Tobe 1990). Based on leaf venation and karyomorphology, within the Ulmoideae (Cronquist 1981) are distinguishable the genera *Hemiptelea*, *Planera, Ulmus*, and *Zelkova* on the one hand and *Holoptelea* and *Phyllostylon* on the other (Oginuma et al. 1990).

Within the Celtidoideae (Cronquist 1981; Leroy 1952; Hutchinson 1958; Soepadmo 1977), *Gironniera* may have an isolated position based on karyomorphology: n=14. (Oginuma et al.1990). *Ampelocera* is distinct within the Celtidoideae in having a venation pattern more like the Ulmoideae than the Celtidoideae, as well as having a distinctive flavonoid chemistry (Giannasi 1978), and pollen wall structure (Takahashi 1989). Morphologically and anatomically, *Aphananthe* and *Ampelocera* appear to bridge the Celtidoideae and the Ulmoideae (Manchester 1989).

The Ulmaceae are placed in the Urticales on the basis of ovule position, androecial type, fruit morphology and presence of cystoliths (Berg 1989). The Ulmaceae are separated from other Urticalean families by the combination of woody habit, absence of latex, typically caducous stipules, simple, distichous, often pinnately veined, usually alternate leaves, cymose or fasciculate inflorescences, stamens that are straight in bud, two styles and antropous to amphitropous ovules (Berg 1989; Manchester 1989). Within the Urticales the Ulmaceae have been suggested to be primitive based on evidence from floral anatomy (Sweitzer 1971). Within the Urticales the family (especially Celtidoideae) appears to be most closely aligned with the Moraceae (Manchester 1989).

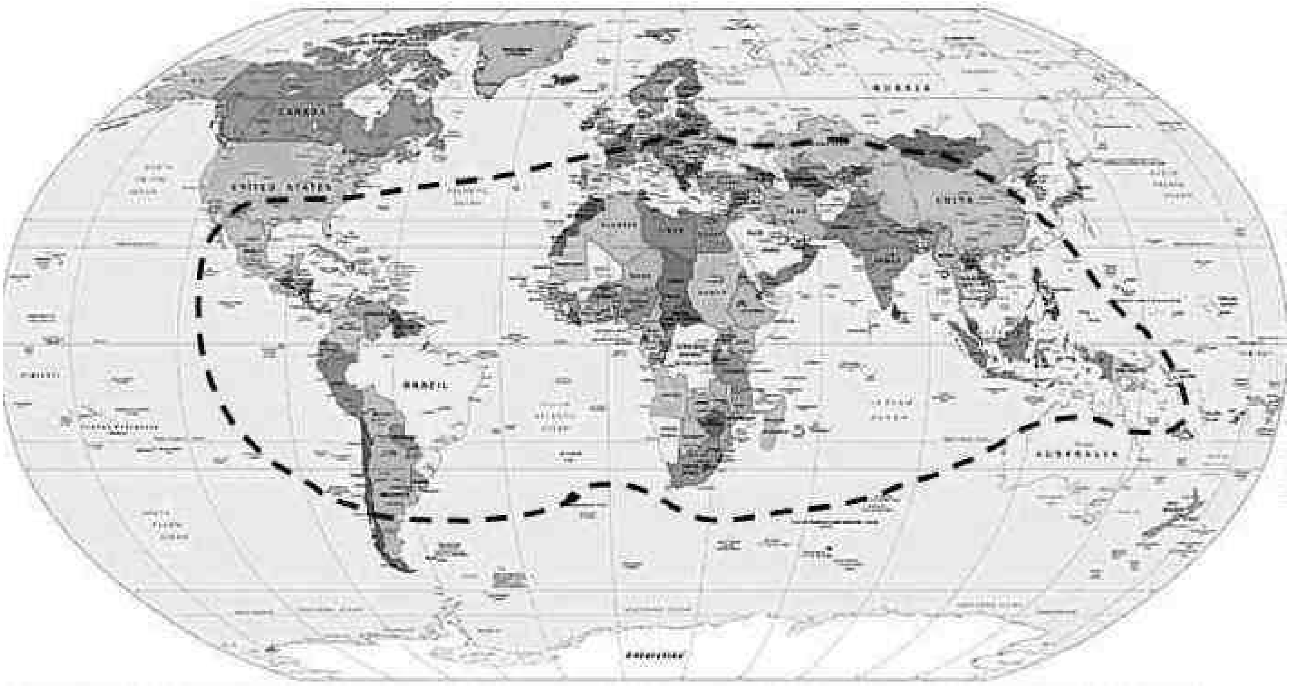


Figure 1.1 Natural distributions of the *Celtis* in the World

1.3 General ecology of *Celtis*

In the flora of Africa, Celtidaceae is a small family with the main genus *Celtis*, represented by c. 8 species mostly in tropical Africa (Letouzey 1972) but in current research 12 species (Sattarian & van der Maesen 2005) can be distinguished. See fig. 1.1 for the distribution of *Celtis* in the world. *Celtis* species range from North Africa (Algeria, Libya and Morocco) to South Africa and Madagascar. The species are found in different ecological settings. Several tree species are found in the rain forest (*Celtis tessmannii, C.mildbraedii)*; some in semi-deciduous forest (*Celtis adolfi-friderici, C. prantlii, C. zenkeri*). Other *Celtis* are shrubs or small trees of rain forest undergrowth (*C. gomphophylla*), or found on the forest/savanna boundary, sometimes in mountain forest (*C. africana*). One species (*C. toka*) is a fairly large tree with a compact crown, living beside streams or planted in villages in the Sudano-Sahelian zone (Flora of Tropical East Africa 1966).

In south Asia, especially Malesian species of *Celtis* may be classified in two rather distinct ecological groups, i.e. *C. philippensis*, *C. tetrandra* , *C. hildebrandii*, *C. latifolia*, *C. luzonica*, *C. paniculata,* and *C. rigescens* are found mainly in lowland forest, both primary and secondary, and are an important constituent of the understorey tree community in in moist areas. The *C. tetrandra* group, which includes *C. rubrovenia*, *C. timorensis*, and *C. philippensis* var. *wightii*, is confined to areas which are subject to a rather pronounced seasonal climate, or they occur in wetter regions; they grow on strongly drained substrates, e.g. rocky shores, limestone. In tune with this environmental preference, the second group shows a more prominent flush-wise growth habit and its species are completely or partly deciduous (Soepadmo 1977).

In South America two groups of species can be recognized, one including *Celtis ehrenbergiana* and *C. chichape,* and the other including *C. brasiliensis* and *C. orthocanthos* centered in southern south America and most of its are components of dry forest. Only *Celtis loxensisi* occurs entirely outside this region and *C. orthocanthos* is apparently an element of more or less humid forest in eastern Brazil (Elias 1970). The main differences between the groups in South America are presence of thorns and geographical distribution (Berg et al. 2001).The species of African *Celtis* are morphologically close to Asian *Celtis* because of their seeds, embryos, absence of thorns, and leaves. South American *Celtis* is characterized by presence of thorns, leaf domatia and by bifurcated or 2-lobed stigmas (Berg et al. 2001).

1.4 General Aims

The major challenge in the taxonomy of *Celtis* has been the difficulty in finding good morphological characters to distinguish the species well. More than 500 published species names are listed in the International Plant Index (IPNI 2004), apparently the most recent database for *Celtis* on a worldwide basis. Because a world monograph is lacking, species concepts vary considerably among regional floras. Current trends have been toward recognizing fewer but more variable species. Although it seems pragmatic, this approach precludes a deeper understanding the systematic relationship among species or their evolution and biogeography. However, relationships of genera and species level within Celtidaceae are still poorly resolved and a monograph of African *Celtis* was lacking. On regional scale *Celtis* has been monographed for Malesia by Soepadmo (1977), for South America by Berg et al. (2001) and for China by Po Shu (2003).

This project was set out to fill some of the gaps in our knowledge, focusing on the following main objectives:

- Revision of the African Species of *Celtis*, study of macro-morphological characters (leaves, indumentum, flowers, and fruits) and micro-morphological characters (pollen, endocarp, and stomata).
- Conduct literature review on Celtidaceae/Ulmaceae systematics and phylogeny.
- Make a conspectus of all *Celtis* species as a contribution to *Celtis* nomenclature.
- Produce an overall molecular phylogenetic hypothesis for Celtidaceae.
- Based on the this phylogeny, verify the status of the African and some widely spread *Celtis* in the framework of a taxonomic revision of the material collected and those on loan from European and other herbaria.
- Describe and classify the genus *Celtis* on the basis of morphological and molecular characteristics

1.5 Outline of the thesis

In chapter 2, the results are presented of a study to clarify the phylogenetic position of *Celtidaceae* with the related families Moraceae, Ulmaceae, Urticaceae.

In chapter 3, I present the results of a study carried out to clarify the phylogenetic position of African *Celtis* with respect to other *Celtis* from different ecological habitat, Phylogenetic relationships of African *Celtis* species.

In chapters 4, 5 and 6 the aim was to study the systematic value of morphological characters in African *Celtis*. Macro-morphological characters (leaves, indumentum, flowers, and fruits) and micro-morphological characters (e.g. pollen, endocarp, stomata) were studied.

In chapter 7, the revision of African *Celtis* is presented, based on the morphological characters and phylogeny and includes a study of one of the species hitherto considered as widespread as the "*Celtis philippensis*"complex".

In chapter 8, the wide-spread "*Celtis philippensis* complex" is studied.

In chapter 9, a conspectus is presented of all *Celtis* occurring in the world, as a contribution to *Celtis* nomenclature.

In chapter 10, the conclusions are given.

Chapter 2

EVOLUTIONARY RELATIONSHIPS OF CELTIDACEAE

R. VAN VELZEN, F.T. BAKKER, A. SATTARIAN & L.J.G. VAN DER MAESEN

Summary

No phylogenetic study published so far has achieved reasonable taxonomic sampling within Celtidoid genera; Sytsma et al. (2002, Fig. 2.1D).Their study represents all genera by one or two species each. An exception is Yesson et al. (2004) based on *trnL* and *ITS* sequences, which has near-complete taxonomic sampling within *Trema*. However, the results of this study did not allow conclusion about the relationships between *Trema* and its closest relative *Parasponia.* Consequently, it is still not clear whether the Celtidoid genera represent monophyletic groups.

The intergeneric relationships within the Celtidoids have little or no support in published DNA-based studies, and differ between all of these studies so far, except for the position of *Aphananthe* as sister to nearly all other Celtidoid genera (Fig. 2.1B, C, D).

In this study, we aim to resolve the phylogenetic uncertainties in the Celtidoids and the Cannabaceae outlined above by analysing an enlarged taxon set in which each genus (except for the monotypic *Pteroceltis*) is represented by at least three species. We will also use model-based tree building methods in addition to parsimony analysis.

2.1 Introduction

The Celtidoids have traditionally been regarded as a subfamily within the Ulmaceae (Engler 1907, and see Chapter 1 for taxonomic history of the family) Ulmaceae are divided into two subfamilies or tribes: one with Ulmus and its relatives and the other with *Celtis* and its related genera. Authors have used various name terminals for these groups, but here we will refer to them as ‘Ulmoids’ and ‘Celtidoids’.

Hutchinson (1967) divided the Ulmacean genera in two tribes according to fruit type: The Celtidoids (*Ampelocera, Aphananthe, Celtis, Chaetachme, Gironniera, Lozanella, Parasponia, Pteroceltis, Trema*, and *Zelkova*) are characterised by fleshy drupaceous fruits. The Ulmoids (*Hemiptelea, Holoptelea, Planera*, *Phyllostylon*, and *Ulmus*) have dry nuts or samaras (Soepadmo 1977).

When looking at the palynology, however, the division should be different: Although *Ampelocera* and *Zelkova* (Celtidoids according to Hutchinson) have fleshy drupes, their pollen type matches that of the Ulmoids (Soepadmo 1977). As molecular phylogenetic studies confirm this pattern, we will follow the same division here, and regard the Celtidoids as comprising *Aphananthe*, *Celtis*, *Chaetachme*, *Gironniera*, *Lozanella*, *Parasponia*, *Pteroceltis* and *Trema* (Leroy 1952, Fu et al. 2003, Hutchinson et al. 1958, Soepadmo 1977, Ulloa & Jørgensen 1995), of which short descriptions are given in Table 2.1. The remaining Ulmaceae genera belong to the Ulmoids and will therefore not be further discussed here: *Ampelocera, Hemiptelea, Holoptelea, Phyllostylon, Planera, Ulmus*, and *Zelkova*.

Phylogenetic studies so far can be summarized as follows. The Ulmaceae are morphologically very close to Moraceae and Urticaceae, but differ from these families by the absence of white or yellowish latex and the presence of 2 equal styles (Soepadmo 1972). These three families have been regarded as members of the order Urticales for a long time already (Engler 1907, Takhtajan 1959, Cronquist 1988) Bessey (1915) placed these families in the superorder Malviiflorae and considered them as families with close affinities to the Malvales, but later authors (Takhtajan 1959, Cronquist 1988) were of the opinion that the Urticales are related to the highly unnatural Cronquist order Hamamelidales (Soepadmo 1972). More recently, molecular phylogenetic studies (Fig. 2.1) have indicated that the relationships of the Urticales are different from what was thought based on morphological characters.

In their seminal paper on the molecular phylogenetics of seed plants, Chase et al. (1993) confirmed that *Celtis*, *Trema*, and *Humulus*, fall into an Urticalean clade with Urticaceae (Boehmeria) and Moraceae (*Morus* and *Ficus*) (Fig. 2.1A). This Urticalean clade is placed in their Rosid I clade, closely related to Rhamnaceae and Rosaceae (Chase et al. 1993), and not to the Malvales (Rosid II). In Chase et al. (1993) Ulmaceae were represented by Celtidoid taxa only.

Subsequent studies, including Ulmoid taxa, point out that Ulmoids are monophyletic and appear sister to all other Urticales (Ueda et al. 1997; Wiegrefe et al. 1998; Song et al. 2001; Sytsma et al. 2002). The Celtidoids, however, appear to be more closely related to the Urticaceae and Moraceae than to the Ulmoids (Ulmaceae s.s., see Figs 2.1B, C, D) (Zavada & Kim 1996; Ueda et al. 1997; Wiegrefe et al. 1998; Song et al. 2001; Sytsma et al. 2002). This would imply the separation of the Celtidoids from the Ulmaceae s.s., as already proposed by Link in 1831, and later supported by Grudzinskaya (1967).

Molecular phylogenetic relationships between the Celtidoids, Moraceae, and Urticaceae appear different in every study published so far, and lacked significant support (Figs 2.1A, B, C). Only the analysis of Sytsma et al. (2002), based on *rbcL*, *trnL-F*, and *ndhF* gene sequences resulted in a robust phylogenetic tree with Celtidoids as sister to a clade comprising Moraceae and Urticaceae (Fig. 2.1D).

Perhaps the most exciting result of all Celtidoid molecular phylogenetic studies published to date is the position of the Cannabaceae within the Celtidoids, rendering the latter paraphyletic. This was first reported in Chase et al. (1993), and has been re-affirmed by all subsequent molecular phylogenetic studies regarding the Celtidoids (Fig. 2.1; Zavada & Kim 1996; Ueda et al. 1997; Wiegrefe et al. 1998; Song et al. 2001; Sytsma et al. 2002). This relationship is corroborated by data from karyology as Cannabaceae and some Celtidoid genera represent the only clades in the Urticales possessing the derived base chromosome number x = 10 (Sytsma et al. 2002). Nevertheless, the sister-lineage of the Cannabaceae within the x = 10 clade (*Celtis*, *Parasponia*, *Pteroceltis*, and *Trema*) is uncertain (Sytsma et al. 2002).

However, monophyly of the Celtidoids s.l. was not well supported upon inclusion of Cannabaceae (Ueda et al. 1997; Wiegrefe et al. 1998; Sytsma et al. 2002). In addition, relationships between the Celtidoid genera themselves remained unclear and phylogenies vary considerably in different studies (Fig. 2.1; Wiegrefe et al. 1998; Song et al. 2001; Sytsma et al. 2002), probably due to low taxonomic sampling.

No phylogenetic study published so far has achieved reasonable taxonomic sampling within Celtidoid genera; Sytsma et al. (2002, Fig. 2.1D) represents all genera by one or two species each. An exception is Yesson et al. (2004) based on *trnL* and *ITS* sequences, which has near-complete taxonomic sampling within *Trema*. However, the results of this study did not allow conclusion about the relationships between *Trema* and its closest relative *Parasponia*. Consequently, it is still not clear whether the Celtidoid genera represent monophyletic groups.

The intergeneric relationships within the Celtidoids have little or no support in published DNA-based studies, and differ between all of these studies so far, except for the position of *Aphananthe* as sister to nearly all other Celtidoid genera (Fig. 2.1B, C, D). In this study, we aim to resolve the phylogenetic uncertainties in the Celtidoids and the Cannabaceae outlined above by analysing an enlarged taxon set in which each genus (except for the monotypic *Pteroceltis*) is represented by at least three species. More specifically we ask the following questions:

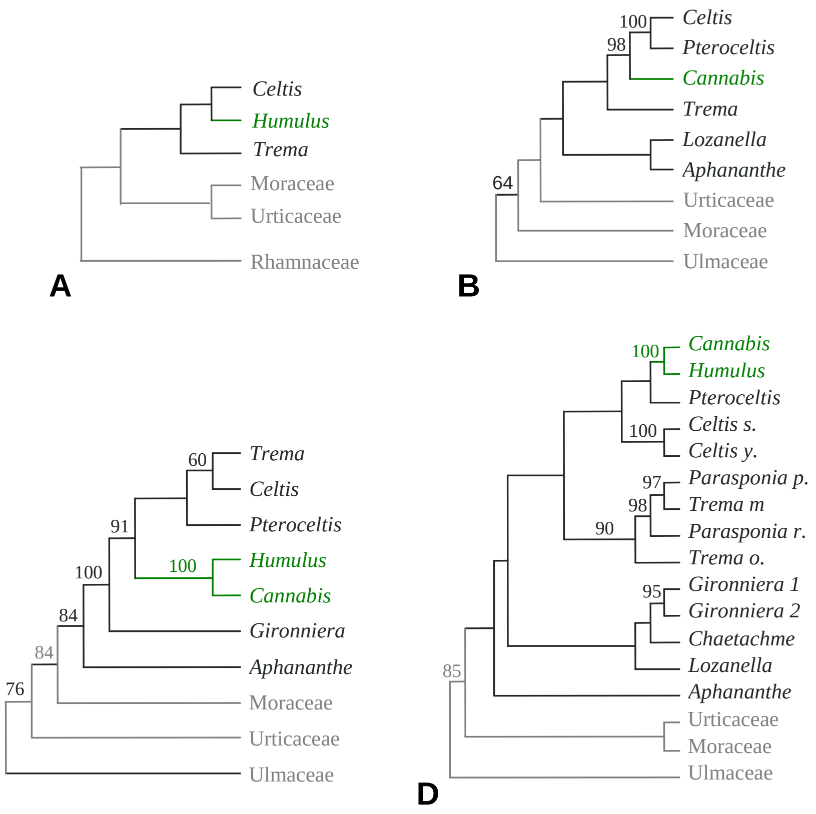


Figure 2.1. Phylogenetic studies so far. Redrawn with Celtidoid taxa in black, Cannabaceae in green, and related families in grey. Node labels indicate bootstrap support values.
A Chase et al. (1993), based on rbcL;
B Wiegrefe et al. (1998), based on cpDNA restriction site mapping;
C Song et al. (2001), based on *MatK*;
D Sytsma et al. (2002), based on *rbcL*.

- Are the Celtidoids sister to a clade with Moraceae and Urticaceae as hypothesised by Sytsma et al. in 2002 (see Fig. 2.1D)?
- Are the different Celtidoid genera monophyletic?
- What are the intergeneric relationships within the Celtidoids?
- What is the phylogenetic position of the Cannabaceae?

In addition, and based on our phylogeny, we will explore evolutionary trends in selected morphological characters (habit, leaf arrangement, flowers, fruit type, leaf margin, pollen type and thorns). One of the first botanists to make hypotheses about such trends was Charles Edwin Bessey (1845-1915). In his paper “The Phylogenetic taxonomy of flowering plants” (1915) he designates a number of dicta: generally accepted principles that were used in the classification of flowering plants in his time. These principles were mainly based on intuitive ideas about polarity of characters, i.e. what states are ancestral and what are derived. In the past decades, the expanding knowledge about phylogenetic relationships of flowering plants has facilitated more formal testing of such hypotheses. Assuming our cladograms reflect phylogenies depicting the relationships between taxa we can thus map traits of interest on a phylogenetic tree, visualising their evolution, after which inferences can be made about evolutionary trends. Here, we want to use our phylogenetic hypothesis in order to determine evolutionary trends of selected morphological characters in the Rosales, in effect testing the validity of some of Bessey’s dicta.

Table 2.1. Genera included in the Celtidoids according to Leroy (1952) Fu et al. (2003), Hutchinson et al. (1958), Soepadmo (1977) and Ulloa & Jørgensen (1995).

Genus	**Spp.**	**Distribution**
Aphananthe Planch. Trees or shrubs, deciduous or semi-deciduous, dioecious or monoecious. Stipules free, caducous, Leaves alternate, margin serrate or entire; 3-veined from base, or pinnately nerved. Flowers unisexual. Male inflor. racemes or cymes. Male flowers: 4-5-merous, tepals imbricate. Female flowers solitary; tepals 4-5, narrow and ± imbricate. Fruit a drupe, 6-15 mm, ovoid to ± globose; cotyledons narrow, involute	5	tropical and subtropical areas of E Asia, Madagascar, Mexico, and Pacific Islands
Celtis L. Trees, deciduous or evergreen, monoecious or polygamo-monoecious, sometimes with axillary spines (subgenus Mertensia, Berg & Dahlberg 2001). Stipules free, caducous or terminal ones persistent and enveloping winter buds. Leaves alternate; margin entire or serrate; 3-veined from base. Inflorescences panicles, racemes, or clustered cymelets. Flowers small, unisexual or bisexual. Inflorescences branched racemes or panicles. Flowers: 4-5 merous, tepals basally slightly connate, imbricate in male flowers, caducous, ovary sessile. Fruit a drupe; 3-25 mm; cotyledons broad, foliacious and variously folded	60	Tropical and temperate areas (see Chapter 3).
Chaetachme Planch. Trees or shrubs, evergreen, monoecious, with zigzag twigs and axillary spines 1.5-2 cm long. Stipules basally connate, caducous, leaving a single transverse scar that completely encircles stem at each node. Leaves alternate, margin entire or sometimes serrate, with spiny apex, venation fine, pinnate. Flowers unisexual or bisexual. Male flowers in a cymose inflorescence; tepals 5, induplicate-valvate; stamens 5. Female flowers solitary; tepals 5; ovary sessile. Fruit a drupe, 8-18 mm, globose or ellipsoid	2	Africa and Madagascar
Gironniera Gaudich. Trees or shrubs, evergreen, dioecious or rarely monoecious. Stipules firm, usually basally connate, enclosing bud, caducous, leaving a single transverse scar that completely encircles stem at each node. Leaves alternate, margin entire or shallowly serrate; venation pinnate. Inflorescences cymes or 1-flowered. Flowers unisexual. Male flowers: tepals 5, imbricate. Stamens 5. Female flowers: tepals 5. Ovary sessile. Fruit a drupe, 5-10 mm compressed or not; cotyledons fleshy and narrow	6	SE Asia, Pacific Islands, Sri Lanka
Lozanella Greenm. Trees or shrubs, evergreen, dioecious. Stipules connate, enclosing bud, caducous, leaving a single transverse scar that completely encircles the stem at each node. Leaves alternate, margin serrate, venation triplinerved at the base. Flowers unisexual. Inflorescences cymose. Flowers 5-merous, tepals imbricate, ovary sessile. Fruit a drupe	2	From Central America (Mexico) to the Andes
Parasponia Miq. Pioneer shrubs to medium sized trees, evergreen, monoecious. Stipules intrapetiolar, connate into a bifurcate unit, caducous. Leaves alternate, margin entire-serrate, venation triplinerved at the base. Flowers unisexual, in a much-branched, many flowered paniculate or thyrsoid inflorescence, 5-merous. Fruit a drupe, 1.5-4 mm, ovoid	5	SE Asia, Pacific Islands
Pteroceltis Maxim. Trees, deciduous, monoecious. Stipules 2, free, linear, caducous. Leaves alternate, serrate, 3-veined from base. Male flowers clustered; tepals 5, imbricate; stamens 5. Female flowers solitary; tepals 4, lanceolate; ovary laterally compressed. Fruit a broadly winged nut, 1-1.7 cm; cotyledons broad	1	China
Trema Lour. Pioneer trees or large shrubs, evergreen, monoecious or polygamo-monoecious. Stipules 2, free, caducous. Leaves alternate; denticulate; usually 3(-5)-veined from base (venation pinnate in *T. laevigata*). Inflorescences subsessile. Male flowers: (4 or) 5-lobed; tepals incurved, valvate, or ± imbricate. Stamens equal in number to tepals. Female flowers: (4 or) 5-lobed. Ovary sessile. Fruit a drupe, 1.5-5 mm, elliptic to ± globose; cotyledons narrow	15	Tropical and subtropical areas

Markers used. In this study, we use the commonly-used cpDNA regions *rbcL* and *trnL-F* as source of phylogenetic markers. The *rbcL* gene codes for the large subunit of ribulose-1,5 bisphosphate carboxylase/oxygenase (McIntosh et al. 1980). Because *rbcL* is a coding region, molecular evolution of this marker is relatively constrained or ‘slow’, and it has been used in various studies focusing on higher-level plant relationships such as families, orders and phyla (see e.g. Chase et al. 1993; Manhart 1993; Sytsma et al. 2002) The *trnL-F* marker consists mainly of two non-coding regions (the *trnL* intron and the *trnL-F* intergenic spacer, see Fig. 2.2), that share a number of molecular evolutionary properties such as the amount of length variation and the amount of simple repeat motifs (Borsch et al. 2003). It is regarded as relatively ‘fast evolving’ and is consequently used in studies at the generic and species level (e.g. Bakker et al. 1999; Hadiah et al. 2003; Yesson et al. 2004).

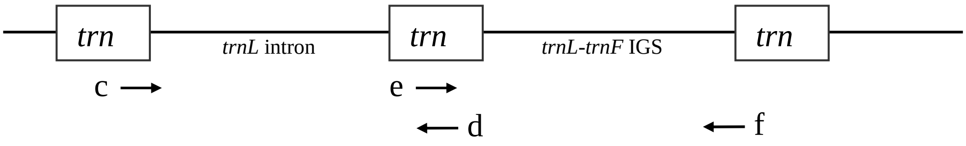


Figure 2.2. Map of the *trnL-F* region. Letters indicate the positions of the used primers (after Taberlet et al. 1991).

It is important to note, however, that the concept of distinguishing ‘slow’ and ‘fast’ evolving genes often considers average amounts of variability in the region under study, rather than picturing rates at individual sites. As the latter are the actual source of variation, a ‘slow’ evolving gene can have its variable positions (e.g. the 3rd codon positions in coding regions) evolving at rates similar to the rates at most individual positions in a ‘fast’ evolving gene (Källersjö et al. 1998; Borsch et al. 2003). Similarly, variable selective constraints on conserved structural elements within ‘fast’ non-coding regions (e.g. stem regions) can produce phylogenetic signal above the species and generic levels (Kelchner 2002, Borsch et al. 2003). For example, the *trnL-F* region has been used to resolve the deep level phylogeny of the basal angiosperms by Borsch et al (2003). The *rbcL* region was used by Drábkovà et al. (2003) for elucidating the phylogenies of the two sister genera *Juncus* and *Luzula* (Juncaceae). Analyses based on a combination of these two markers have proven successful in resolving phylogenies at the familial and sub familial levels within the Urticalean Rosids (e.g. Richardson et al. 2000; Sytsma et al. 2002).

Non-coding regions such as *trnL-F* usually show significant length variation due to various insertion or deletion events (indels), resulting in gaps in the sequence alignment. Simmons & Ochoterena (2000) suggest that gaps should be coded as characters in phylogenetic analyses. They argue that, because gaps are part of the aligned pattern that may be phylogenetically informative, to exclude gap characters is to discard data. Indeed, in several studies the distributions of gaps provide a valuable source of phylogenetic information (see e.g. Bakker et al. 1999; Hadiah et al. 2003).

2.2 Material & methods

Taxon sampling. We have sampled 70 accessions of Celtidoids and Cannabaceae, comprising around 57 species; all genera and about 62 % of all species are represented. Of these accessions, 28 are from GenBank, and 42 are new. The new accessions are from herbarium material (26) and from silica-dried leaf material coming from botanical gardens (15). In addition the dataset contains GenBank accessions of Urticaceae (13), Cecropiaceae (3), Moraceae (11), Ulmaceae s.s. (6, one new), Rhamnaceae (9), Elaeagnaceae (3), Rosaceae (7), and Fagales (10). For a list of all taxa, see Appendix 1. This taxon set of 134 taxa was used for the examination of the phylogenetic signal in the different dataset partitions and the plotting of morphological characters, with *Nothofagus* as outgroup. All other analyses were based on a taxon set of 118 taxa; excluding Fagales and Rosaceae, but including Dryas (Rosaceae).

DNA extraction, amplification, and sequencing. Total genomic DNA was extracted from herbarium material or silica-dried leaves (8-10 mg) using the modified CTAB extraction protocol of Doyle & Doyle (1987), following the DNA extraction protocol of the Biosystematics Group. Extraction of DNA from difficult herbarium material was also attempted using the DNeasy plant extraction kit (Qiagen), but without success. Concentration and quality of the extracted DNA was measured using the Nanodrop® ND-1000 spectrophotometer.

Amplification was performed in a volume of 50 µL containing 37-123 ng genomic DNA, 0.2 µM of each primer and each dNTP, 3 mM MgCl2, 75 mM Tris-HCL, 20 mM (NH4)2SO4, 0.01% Tween 20, and 1.5 unit Taq Polymerase. The used primer sequences are listed in table 2.1: The rbcL gene was amplified in two parts: rbcL1 and rbcL2, using primer pairs 1F–724R and 636F–1460R, respectively (Fay et al. 1997, Renner 1998). For *rbcL* the following temperature profile was used: 30 cycles of 1 min. denaturation at 94°C, 1 min. annealing at 50°C and 1 min. extension at 72°C, followed by one cycle of 7 min. at 72°C. The *trnL-F* region was amplified in one part using primers c and e, or in two parts using primer combinations c–d and e–f when amplification in one part was unsuccessful (Taberlet et al. 1991). The following temperature profile was used: 1 min. denaturation at 94°C, 1 min. annealing at 53°C, 2 min. extension at 72°C, followed by one cycle of 7 min. at 72°C. After visual inspection on a 1%-agarose gel, fragments were cleaned using Qiaquick purification columns (Qiagen) following the manufacturer's protocol and eluted in 20, 30 or 40 µL MQ water, depending on the quality of the bands on the agarose gel.

Cleaned fragments were sequenced using a fluorescent dye-labelled sequencing reaction (DYEnamic™ ET Terminator Cycle Sequencing Kit; Amersham Biosciences), and the high-throughput ABI sequencing facilities at Greenomics™, Wageningen. All generated sequences will be submitted to GenBank.

Table 2.2. Primer sequences used for amplification and sequencing of the markers *rbcL* and *trnL-F*.

marker	primer	primer sequence	reference
rbcL	1F	`5′-ATGTCACCACAAACAGAAAC-3′`	Fay et al. (1997)
	636F	`5′-GCGTTGGAGAGATCGTTTCT-3′`	Fay et al. (1997)
	724R	`5′-CATGTACCTGCAGTAGC-3′`	Renner et al. (1998)
	1460R	`5′-CTTTTAGTAAAAGATTGGGCCGAG-3′`	Renner et al. (1998)
trnL-F	c	`5′-CGAAATCGGTAGACGCTACG-3′`	Taberlet et al. (1991)
	d	`5′-GGGGATAGAGGGACTTGAAC-3′`	Taberlet et al. (1991)
	e	`5′-GGTTCAAGTCCCTCTATCCC-3′`	Taberlet et al. (1991)
	f	`5′-ATTTGAACTGGTGACACGAG-3′`	Taberlet et al. (1991)

Sequence and phylogenetic analyses. Sequences were assembled and edited using the STADEN version 1.5.3 (Staden et al. 2003), and aligned using the ClustalW multiple alignment option in the BioEdit sequence alignment editor 7.0.4.1 (Hall 1999). Further refinement of the alignment was done by eye using the same software, and MacClade version 4.07 (PPC) (Maddison & Maddison 2000). Insertions and deletions (indels) of the *trnL-F* region were coded following the 'simple indel coding' protocol as described by Simmons & Ochoterena (2000).

All parsimony analyses were carried out in PAUP* (Swofford 2000). PAUP* version 4.0b10 for Macintosh (PPC) was used, on a Macintosh G3. The parsimony jackknife and the MP search were done in PAUP* version 4.0b10 for Macintosh (PPC/ALTIVEC) on a Macintosh G5. As an alternative to PAUP*, the program TNT 1.0 (Goloboff et al. 1999) was also used, because it is known to be more efficient in finding MP trees for large taxon sets (Hovenkamp 2004).

Parsimony analyses. Jackknife support analysis was performed with settings according to the best results of a jackknife settings test with 118 taxa (van Velzen et al. in prep.). The majority-rule consensus tree was imported in PAUP* to calculate branch lengths under MP. Clade support values >60% were re-entered by hand. This resulted in a phylogram of the jackknife majority-rule consensus tree.

The MP search was done in two steps: In order to explore different parts of tree space, first 10.000 trees were generated by a heuristic MP search with 1000 random-addition replicates, and saving 10 trees per replicate (10 trees held during stepwise addition, TBR branch swapping). These were used as starting trees for a second MP search, with TBR branch-swapping on all starting trees. After 2.5676 x E^{09} rearrangements, memory was full, containing 125,700 trees of length 3,028. These trees were swapped to completion in 8 more hours, without finding shorter trees.

In the program TNT, the ‘new technology search’ analysis was used, employing sectorial search, ratchet, drift, and tree fusing, with default settings.

Model selection. To select the optimal models for the different partitions (*rbcL*, *trnL-F*, *rbcL12*, and *rbcL3*, see Fig. 2.3), MrModelTest 2.2 (Nylander 2005): a modified version of Modeltest 3.6 (Posada & Crandall 1998) was used in combination with PAUP*. The models were selected according to the hierarchical likelihood ratio test (hLRT), and the Akaike information criterion (AIC).

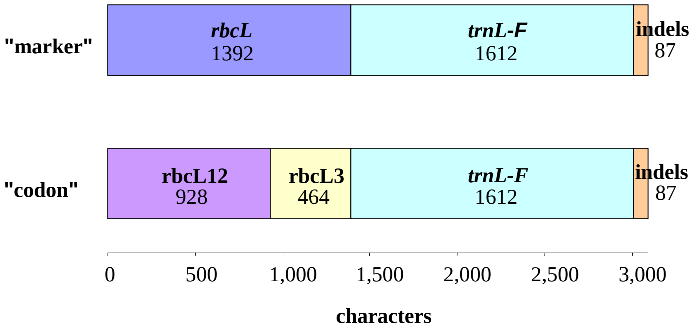


Figure 2.3. Partitioning of the dataset for the Bayesian analyses. Number of characters is shown for each partition and at the scale bar. The “marker” analysis has 3 partitions, according to the markers *rbcL* and *trnL-F* and the coded indels. The “codon” analysis has 1 partition more because the *rbcL* marker is further partitioned according to the codon positions.

Bayesian analyses. Bayesian analyses were performed in MrBayes version 3.1.1 (Ronquist 2003) on a Pentium PC with 1 GB RAM. Analyses consisted of two simultaneous runs of 15 million generations with a sample frequency of 100. Each run consisted of 3 chains (2 chains heated).
Two analyses were done; one with partitioning according to marker (*rbcL*, *trnL-F*, indels), hereafter referred to as “marker”, and another with rbcL partitioned even further to codon positions (*rbcL12*, *rbcL3*, *trnL-F*, indels), hereafter referred to as “codon”;. Models of the partitions were set according to the ones selected by MrModeltest. For the priors and proposal rates we used the default settings of MrBayes.

Morphological character optimisation. Morphological characters were selected based on assessment of their level of information for clades within the Urticalean Rosids. These characters (see appendix 2) were then mapped onto a jackknife majority-rule consensus tree based on 134 taxa and all dataset partitions (100 replicates with 37% of the characters deleted in each replicate (“jac” resampling), 1 tree held during stepwise addition, TBR branch-swapping, 10 trees saved per replicate, 1 random-addition sequence replicate) using Mesquite version 1.05 (Maddison & Maddison 2005), with parsimony as the ancestral state reconstruction method.

2.3 Results

Alignment of the rbcL marker was straightforward because there was no length variation. The *trnL-F* region, on the other hand, showed considerable length variation within our dataset. The longest complete *trnL-F* sequence was 986 base pairs long (Ampelocera), the shortest sequence 712 base pairs long (Cannabis). The final alignment of the *trnL-F* region became almost twice as long (1692 base pairs), because various insertion and deletion events (indels) resulted in gaps in the alignment, ranging in length from 1 to 377 base pairs.

Because of the high taxonomic sampling in the Celtidoids, some indels could be identified as synapomorphies for certain species within that group. Almost all Celtidoids and Cannabaceae share a large deletion in the *trnL-F* intergenic spacer (IGS) region, and two more indels. Only Aphananthe still contains this sequence; this genus is lacking another large part of the *trnL-F IGS* and three more indels. The Celtidoid genera *Gironniera* and *Lozanella* both have their unique deletion in the trnL intron and three more indels each. *Cannabis* has one major deletion in the trnL intron. Within the Celtidoid genus *Celtis*, 12 sequenced species share a major deletion in the trnL intron; *Celtis gomphophylla* and *C. durandii* share a deletion in the *trnL-F IGS* as well as one other indel in the trnL intron. Dataset partition signal testing. For a summary of the results of the dataset partition tests, see table 2.3.

Table 2.3. Dataset partition signal testing: summary of the number of characters, informative characters (absolute and relative), the number of nodes (>50% jackknife support) found, and the number of nodes found per character.
* Minimum % based on longest sequence length of 986 base pairs (*Ampelocera*).

taxa	**tested dataset partition(s)**	**characters**	**informative characters**		**nodes**	**nodes / character**	**nodes / taxon**
82	*rbcL*	1392	292	21%	51	0,037	0,62
82	rbcL12	928	70	8%	16	0,017	0,20
82	rbcL3	464	222	48%	50	0,108	0,61
82	*trnL-F*	1612	464	47%*	59	0,037	0,72
82	indels	87	73	84%	23	0,264	0,28
82	*rbcL* +*trnL-F*	3004	756	25%	65	0,022	0,79
82	*rbcL* +*trnL-F* +indels	3091	829	27%	65	0,021	0,79
104	*rbcL* +*trnL-F* +indels	3091	860	28%	82	0,027	0,79
122	*rbcL* +*trnL-F* +indels	3091	874	28%	80	0,026	0,66
134	*rbcL* +*trnL-F*	3004	818	27%	84	0,028	0,63
134	*rbcL* +*trnL-F* +indels	3091	905	29%	87	0,028	0,65

82 taxa The *rbcL* partition has 1392 characters of which 292 (21%) are parsimony informative for the 82 taxa analysed. The majority-rule consensus tree has 51 nodes. When looking only at *rbcL12*, it contains 928 characters, of which 70 (8%) are informative, and the majority-rule consensus tree has just 16 nodes. The phylogenetic signal in the *rbcL3* partition is much better; it contains 464 characters of which 222 (48%) are informative, and the majority-rule consensus tree is almost identical to that of rbcL as a whole (50 nodes). The *trnL-F* region, with an aligned length of 1612

characters, contains 464 informative characters, which is at least 47% considering that the longest sequence (*Ampelocera*) is 986 characters long. The jackknife majority-rule consensus tree based on *trnL*-F alone has 59 nodes. The coded indels of the *trnL-F* region provide another 87 characters, 73 (84%) being informative for the 82 taxa. The majority-rule consensus tree of a jackknife analysis based on these coded indels alone has 23 nodes.

When combining the *rbcL* and *trnL-F* partitions (3004 characters, of which 756 (25%) informative), the majority-rule consensus tree is even better resolved with 65 nodes. The addition of the coded indels does not change the resolution of 65 nodes.

104 and 122 taxa. Excluding only the taxa missing the *rbcL* marker (104 taxa), combining all partitions (both markers and the indels: 3091 characters, of which 860 (28%) informative) produces a jackknife majority-rule consensus tree with 82 nodes (a mean number of 0.79 nodes per taxon).

When excluding taxa missing the *trnL-F* marker (122 taxa, 3091 characters, of which 874 (28%) informative), the number of nodes is 80 (a mean number of 0.66 nodes per taxon)

134 taxa. With all taxa included, combining the *rbcL* and *trnL-F* markers (3004 characters, of which 818 (27%) informative), yields a jackknife majority-rule consensus tree with 84 nodes. Adding the coded indels characters (3091 characters, of which 905 (29%) informative) results in more resolution in the jackknife majority-rule consensus tree: 5 additional nodes above 50% are found, adding up to a total number of 87 nodes (a mean number of 0.65 nodes per taxon).

The topology of the NNI jackknife based on 134 taxa. shows a clade of Fagales (95% jackknife support) as sister to the Rosales. Rosaceae are monophyletic (95% support), and are sister to all other Rosales (78% support). The latter clade contains a polytomy with *Barbeya* and *Dirachma*, Elaeagnaceae, Rhamnaceae and the Urticalean Rosids. Consequently, we decided that for all subsequent analyses the taxon set could be limited to the Rosales only, and with Rosaceae (Dryas as only representative) as outgroup, in order to make these analyses faster. This means exclusion of the Fagales and all Rosaceae except *Dryas*, leaving a taxon set of 118 taxa.

2.3.1 Parsimony analyses

Jackknife. The phylogram of the jackknife majority-rule consensus tree (5000 replicates, employing TBR branch-swapping, 1 random-addition sequence replicate, saving 1 tree per replicate) is shown in Fig. 2.4. The families Rhamnaceae, Ulmaceae, Moraceae, Urticaceae (with Cecropiaceae), and Cannabaceae are all strongly supported monophyletic groups. Ulmaceae are sister to the remaining Urticalean Rosid families. The latter clade is also very strongly supported (100%). The Celtidoids (with Cannabaceae) appear as sister to the Urticaceae and Moraceae, but support is still weak to moderate: Moraceae and Urticaceae together receive only 61% jackknife support, and the Celtidoids s.l. (with Cannabaceae) receive 72% support. (Fig.2.4). The moderate support value for the Celtidoids s.l. is due to the uncertain position of Aphananthe; the clade comprising all other Celtidoids s.l. receives very strong support (99%).

Most Celtidoid genera are very strongly supported clades (96-100%); only *Parasponia* and *Trema* are still unresolved, and *Celtis* is monophyletic except for two unresolved species. *Aphananthe* appears as sister to all other genera, then *Lozanella*, and *Gironniera* appears as sister to an unresolved but very strongly supported clade containing Cannabaceae, *Celtis*, *Chaetachme*, *Parasponia*, *Pteroceltis*, and *Trema*. Within this clade, *Trema* and *Parasponia* form a strongly supported group (92%). Within that group, relationships are largely unresolved, but there is a clade with *P. andersonii*, *P. simulans*, *P. melastomatifoli*a, and one accession of *P. rigida* (81%) *Cannabis* and *Humulus* appear as sister genera. *Pteroceltis* is sister to *Chaetachme* (96%). Within *Celtis*, subgenus *Mertensia* -as described by Berg & Dahlberg (2001) is a monophyletic group (98%), related to several African species (81%). All Asian and temperate *Celtis* species, together with *C. africana*, receive very strong support (100%) (Fig. 2.4).

Figure 2.4 A.

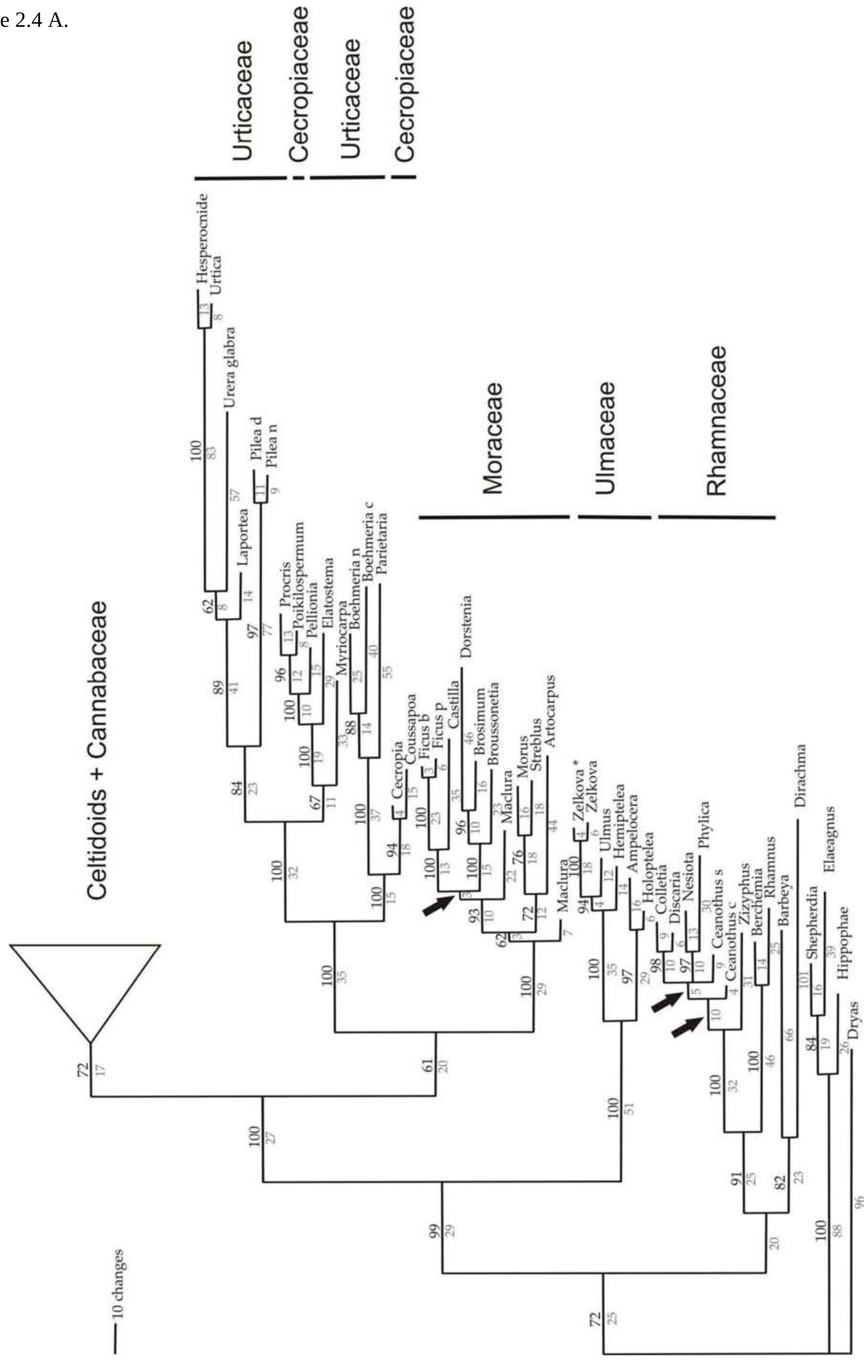
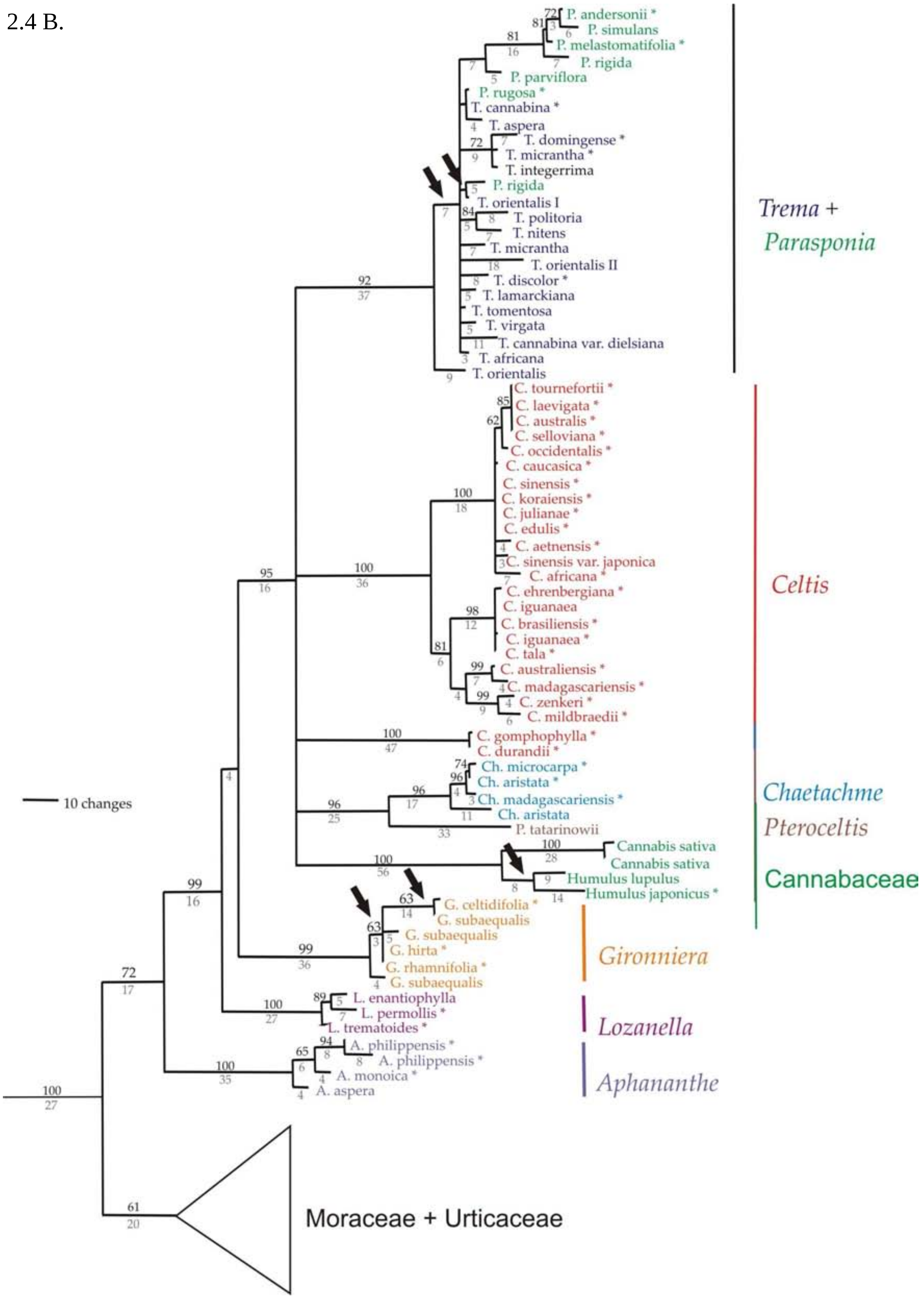

Urticaceae
Cecropiaceae
Urticaceae
Cecropiaceae
Moraceae
Ulmaceae
Rhamnaceae
Celtidoids + Cannabaceae
Hesperocnide
Urtica
Urera glabra
Pilea d
Pilea n
Laportea
Procris
Poikilospermum
Pellionia
Elatostema
Myriocarpa
Boehmeria n
Boehmeria c
Parietaria
Cecropia
Coussapoa
Ficus b
Ficus p
Castilla
Dorstenia
Brosimum
Broussonetia
Maclura
Morus
Streblus
Artocarpus
Maclura
Zelkova *
Zelkova
Ulmus
Hemiptelea
Ampelocera
Holoptelea
Colletia
Discaria
Nesiota
Phylica
Ceanothus s
Ceanothus c
Zizyphus
Berchemia
Rhamnus
Barbeya
Dirachma
Shepherdia
Elaeagnus
Hippophae
Dryas
10 changes

Figure 2.4. Phylogram of the parsimony jackknife majority-rule consensus tree (5000 replicates, TBR branch-swapping, multrees off). based on 118 taxa, the *rbcL* and *trnL-F* markers and the coded indels. Species marked with an * represent new sequences generated in this study. Node labels above branches show the jackknife support values (only nodes with support >63% are shown here)., node labels below branches indicate the branch lenhths (only changes >3 are shown). Arrows mark nodes that collapse in the MP strict consensus tree (all of these nodes received only weak support: 50-63%). A Without Celtidoids and Cannabaceae; B Celtidoids and Cannabaceae included.

Figure 2.4 B.



Shortest tree search. During the heuristic search, shortest trees of score 3028 were already found within the 1000 random-addition replicate search designed for generating the 10000 starting trees. The starting trees had lengths of 3028 to 3037, and the subsequent swapping on all these trees did not produce any shorter tree before tree buffer overflow, containing 125700 trees of length 3028. Employing the program TNT did not result in any shorter tree, and we have confidence in the fact that these trees are actually most parsimonious. The strict consensus tree of all 125700 equally parsimonious trees is almost identical to the parsimony jackknife tree, but is a little less resolved; 7 nodes that received weak support (50-63%) in the jackknife, collapsed in the MP strict consensus tree, as indicated by the arrows in (Fig. 2.4). Only one node in the MP tree, grouping *T. orientalis* II, and *T. lamarckiana* with the clade comprising *T. domingense*, *T. micrantha*, and *T. integerrima*, was not already found in the jackknife analysis.

2.3.2 Bayesian analyses

Using default settings, Bayesian MCMC chains did not have sufficient mixing: The proportions of successful exchanges between the chains were very low (0.00 – 0.01), indicating that the default temperature for the heated chains (T=0.20) was too high (Ronquist & Huelsenbeck 2004). The acceptance rates for the proposed moves in the "cold" chain were all within the recommended range of 10 – 70%, except for the moves of the state frequencies (6.5 – 8.5%), and for the alpha shape parameter for the *rbcL* partition.

Therefore, analyses were re-run after some adjustments of the proposal parameters and the temperature. The proposal parameter for the state frequencies (statefreq) was set from the default 300 to 600, in order to make proposals les bold (when using a dirichlet parameter, higher proposal parameter values will decrease the variance in the proposals). The proposal rate for the state frequencies was left at its default value of 1. The proposals for the alpha shape parameter were all left at their default values, because it was unclear which parameters should be adjusted. The temperature for the incrementally heated chains was set to T=0.05, yielding heats of 1.00 (cold chain), 0.95 and 0.91. With these settings, the Bayesian MCMC chains performed better:

"Marker" analysis. For the analysis with partitioning according to the markers (*rbcL*, *trnL-F*, indels), the proportions of successful exchanges between the chains were improved: still a low 0.04-0.05 for the exchange between the two heated chains, but a very acceptable 0.30 for the exchange between the heated chain and the cold chain, indicating that at least the first heated chain was efficiently exchanging states with the cold chain; a prerequisite for proper mixing. The acceptance rate for the state frequency parameters were also increased to an acceptable 13.6% – 16.5%. The acceptance rate for the alpha shape parameter for the *rbcL* partition remained at a low value of 4.5% because its proposal parameter was not adjusted.

After 15 million generations, the standard deviation of the split frequencies in the simultaneous two runs was 0.008, indicating that the runs had converged on the same posterior probability distribution The rough plots of generation versus log likelihood showed that the two runs reached stationarity at different times. Run 2 had a burn-in of 5000, which is roughly 3% of the total 15,000 samples. Run 1, however, had a burn-in of 35,000 samples (23%). Because it is not possible to use different burn-in settings for each run, 35,000 samples were discarded as burn-in before calculating the model parameter values, the trees, and branch lengths. The calculations were thus based on 230,000 (2*115,000) samples taken from 11,500,000 generations.

"Codon" analysis. The analysis with *rbcL* partitioned to codon positions (*rbcL12*, *rbcL3*, *trnL-F*, indels) was done with the same adjustments to the temperature and the state frequencies proposal parameter. The proportions of successful exchanges between the chains were 0.35 for the exchange between the two heated chains, and 0.40 between the heated chain and the cold chain. The acceptance rates were 13.6% – 29.4% for the state frequency parameters, and 10.2-51.8% for the alpha shape parameters.

After 15 million generations, the standard deviation between the split frequencies in the simultaneous two runs was 0.007, indicating that the runs had converged on the same posterior probability distribution

The rough plots of generation versus log likelihood showed that the two runs already reached stationarity after 1000 samples which were discarded as burn-in. Calculations were thus based on 298,000 (2*149,000) samples taken from 14,900,000 generations. Bayesian clade credibilities for the 24 scored clades were overall higher than the jackknife support frequency, with a difference of 3 – 32 (“marker” analysis) or 5 – 44 (“codon” analysis), depending on the clade. The only exception to this pattern is the clade credibility value for the Celtidoids excluding *Aphananthe* and *Gironniera* which is 5 below the jackknife frequency. The Bayesian majority-rule consensus tree was also more resolved than the jackknife majority-rule consensus tree, with an additional 5 or 6 nodes with clade credibilities above 50 (89 and 90 nodes in the Bayesian “marker” and “codon” trees, versus 84 nodes with support values above 50% in the jackknife tree, see table 2.4).

The topology of the Bayesian majority-rule consensus trees (Fig. 2.5) was very similar to the jackknife majority-rule consensus tree. Apart from the following differences, there was no conflict between the Bayesian and parsimony jackknife trees: Within Urticaceae, the genus *Pilea* had moved from the clade with *Urtica*, *Hesperocnide*, *Urera*, and *Laportea*, to the clade with *Myriocarpa*, *Elatostema*, *Pellionia*, *Procris*, and *Poikilospermum* (53% and 53% p.p. for the “marker” and “codon” analyses, respectively). The sister to *Urtica* and *Hesperocnid*e has changed from *Urera* to *Laportea* (54% and 64% p.p.). In the Moraceae, *Maclura pomifera* has moved from a position as siter to all other Moraceae to a position as sister to *Morus*, but this was in the “codon” analysis only (66% p.p.). In the Celtidoids, *Celtis zenkeri* and *C. mildbraedii* had become sister to *Celtis* subgenus *Mertensia* (65% and 57% p.p.) sister to the other African *Celtis*; *C. australiensis* and *C. madagascariensis*. (This name is replaced by *C. malagasica*, see chapter 7). Thus, Neotropical and African *Celtis* being sisters, the African representatives became paraphyletic.

The additional nodes found by the Bayesian MCMC analyses comprise a few worth mentioning here: Elaeagnaceae had moved from an unresolved position to the clade with Rhamnaceae, *Barbeya*, and *Dirachma* (85% and 95% p.p.). The two African *Celtis* species that were unresolved in the jackknife consensus tree; *C. gomphophylla* and *C. durandii*, became sister to the Cannabaceae (94% and 74% p.p.). Within *Trema*, both *T. lamarckiana* and *T. orientalis* II became related to the clade comprising *T. domingense*, *T. integerrima*, and *T. micrantha* (87% and 73%)

Table 2.4. Number of nodes (>50% jackknife support or Bayesian p.p. value) and values of 24 selected clades for the parsimony jackknife and the Bayesian analyses.

Mor+Urt	62	62	93	96
Moraceae	100	100	100	100
Broussonetia-Ficus	59	59	89	89
Maclura-Ficus	93	93	99	100
Myriocarpa-Procris	68	69	63	66
Celtidoids+Cannabaceae	74	74	97	99
A. philippensis+monoica	66	66	98	95
Celtidoids+Cannabaceae *(-A)*	99	99	100	100
Celtidoids+Cannabaceae *(-A&L)*	58	58	68	53
Celtidoids+Cannabaceae *(-A&L&*	95	95	100	100
Parasponia+Trema	92	93	100	100
Humulus	53	53	78	98
Chaetachme+Pteroceltis	97	97	100	100
Chaetachme	96	96	100	100
Celtis (Old World)	81	81	97	99
Celtis Mertensia	97	98	100	100
Celtis (temperate)	63	63	81	79

Figure 2.5 A.

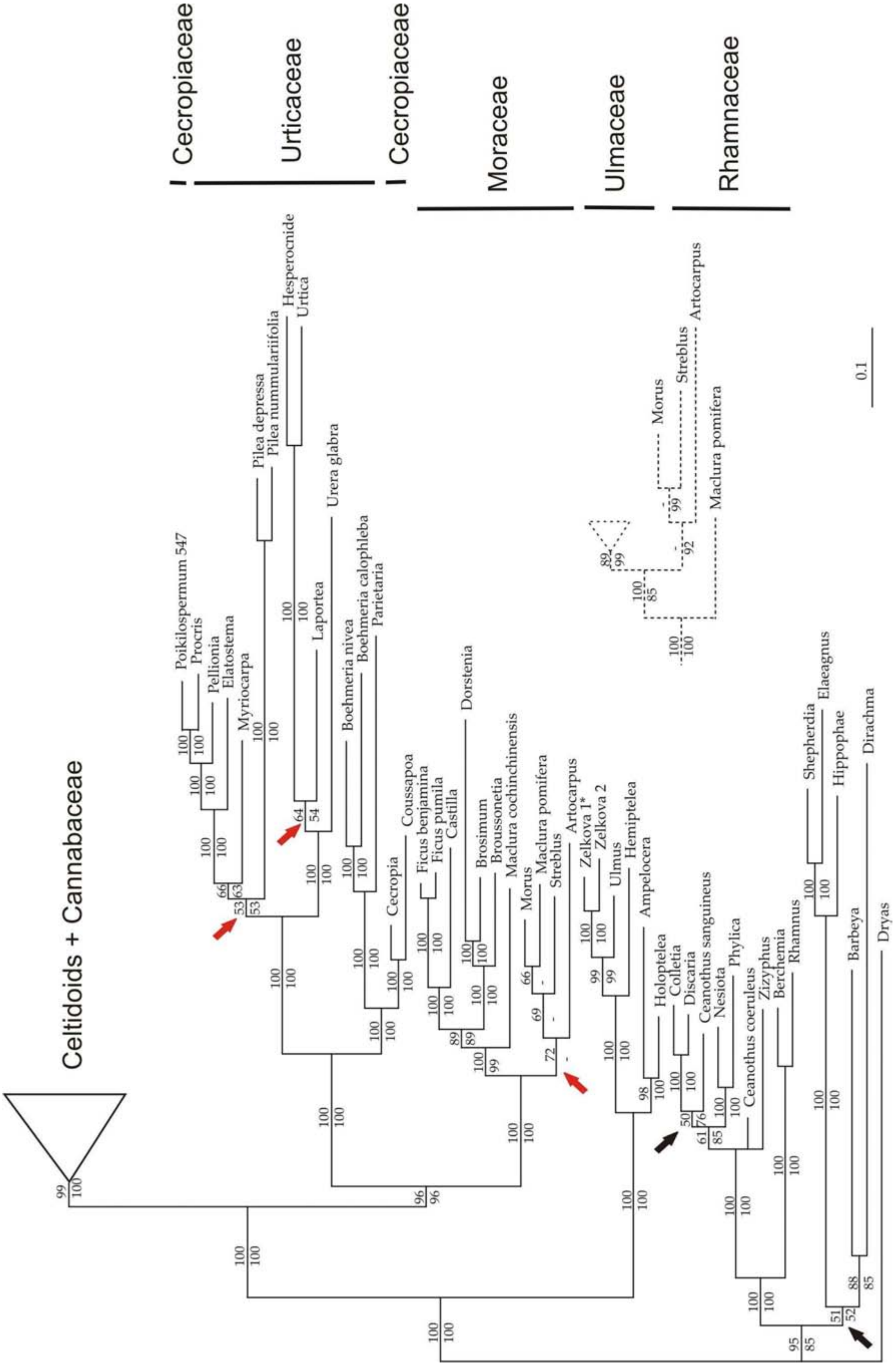
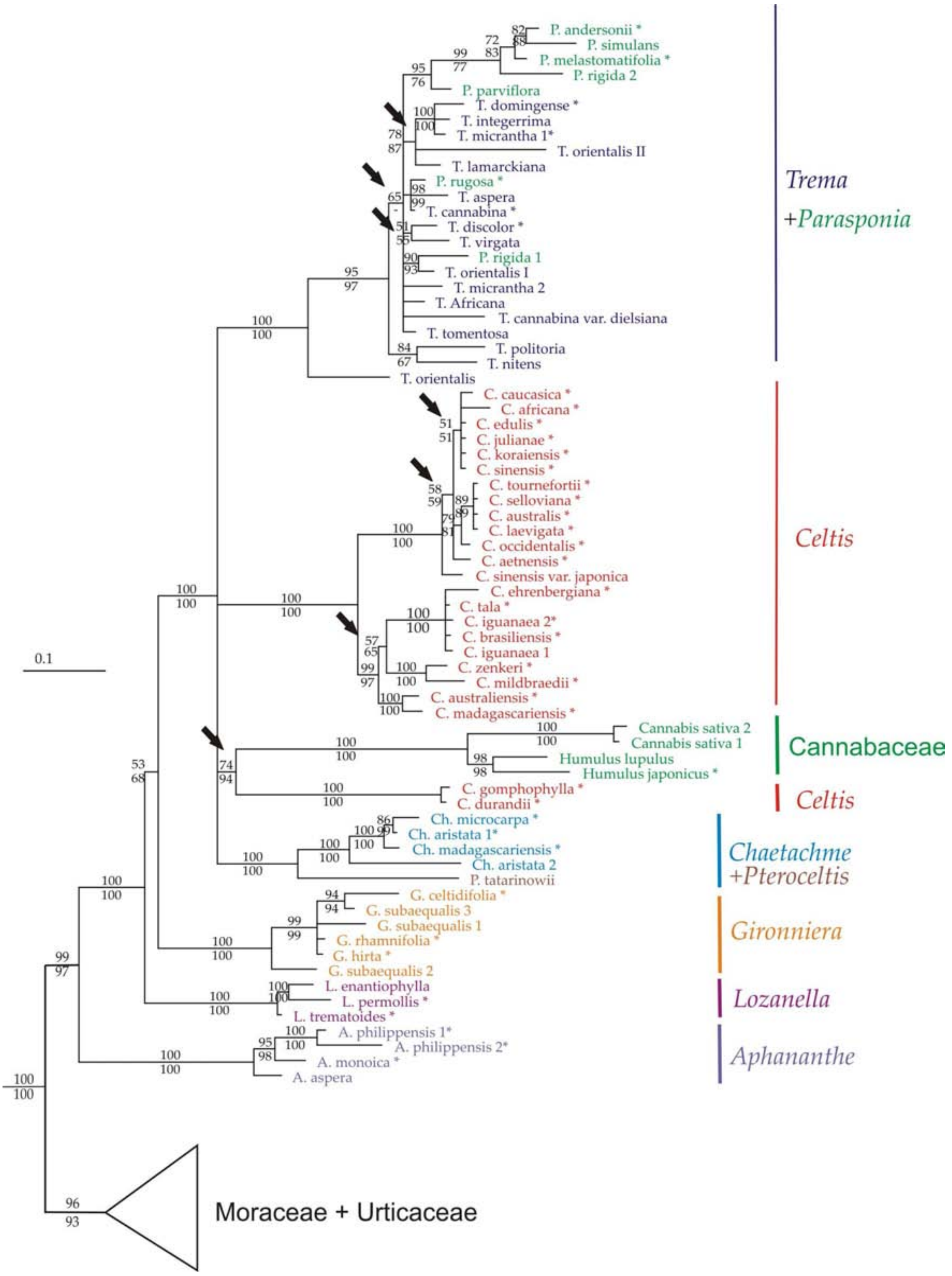

Celtidoids + Cannabaceae
Cecropiaceae
Urticaceae
Cecropiaceae
Moraceae
Ulmaceae
Rhamnaceae
Poikilospermum 547
Procris
Pellionia
Elatostema
Myriocarpa
Pilea depressa
Pilea nummulariifolia
Hesperocnide
Urtica
Laportea
Urera glabra
Boehmeria nivea
Boehmeria calophleba
Parietaria
Cecropia
Coussapoa
Ficus benjamina
Ficus pumila
Castilla
Dorstenia
Brosimum
Broussonetia
Maclura cochinchinensis
Morus
Maclura pomifera
Streblus
Artocarpus
Zelkova 1*
Zelkova 2
Ulmus
Hemiptelea
Ampelocera
Holoptelea
Colletia
Discaria
Ceanothus sanguineus
Nesiota
Phylica
Ceanothus coeruleus
Zizyphus
Berchemia
Rhamnus
Shepherdia
Elaeagnus
Hippophae
Dirachma
Barbeya
Dryas
Morus
Streblus
Artocarpus
Maclura pomifera
0.1

Figure 2.5. Phylogram of the Bayesian majority-rule consensus tree of the “codon” analysis (15 million generations). based on 118 taxa and the rbcL12, rbcL3, *trnL-F* and indel partitions, each with its own model of molecular evolution (see 4.5). Species marked with an * represent new sequences generated in this study. Node labels above branches show the Bayesian clade credibility values of the “codon” analysis, node labels below branches show the Bayesian clade credibility values of the “marker” analysis. Black arrows mark nodes that collapse in the parsimony jackknife majority-rule consensus tree, red arrows indicate conflict with that tree. A Without Celtidoids and Cannabaceae; B Celtidoids and Cannabaceae included.

Figure 2.5 B.



The topologies estimated by the Bayesian "marker" and "codon" analyses were very similar, but some additional nodes were only found in one of the two: The clade with *Chaetachme* and *Pteroceltis* seemed to be sister to the clade with the still unresolved *Trema* + *Parasponia* (only in the "marker analysis: 51% p.p.). In the clade of *Parasponia* + *Trema* without *T. orientalis*, the clade with *T. politoria* and *T. nitens* appears as sister of all other taxa (only in the "codon" analysis: 65%).

2.3.3 Morphological character mapping

Morphological characters were selected based on the level of their variation within the Rosales: characters with a relative high level of conservation within genera or families were selected against characters with too much variation on the generic or species level, such as e.g. fruit shape, leaf size, number of flower parts, or hairs. Fig. 2.6 shows these characters as they were traced over the phylogeny. A table of the scored characters for all taxa can be found in appendix 2.

Habit

See Fig. 2.6 A. Growth habit is a very important character in the identification of plant species groups. The Rosales contain many growth habits, ranging from tiny herbs to tropical canopy trees. We have decided to apply a basic division in growth habit with all herbaceous species scored as herbs, and the woody species further divided into shrubs (branchy trunk and less than 7 meter high) and trees (single trunk, over 7 meter high). Because growth habits (herb; shrub; tree) are not randomly occurring in the different families and genera, it is interesting to see if there is a general evolutionary trend for these characters.

According to Bessey's dicta "Woody stems are more primitive than herbaceous stems, and herbs are held to be derived from trees" (Bessey 1915).

Mapping the habit on the Rosales phylogeny confirms that the ancestral state is a tree. The direct ancestor to the Rosales is uncertain, because the Rosaceae contain many herbs and shrubs, but all other Rosales almost certainly share a treelike ancestor. Within the Rhamnaceae, Elaeagnaceae, *Dirachma* and *Barbeya,* shrubby growth has evolved at least 4 times. Within Moraceae, *Dorstenia* is the only herb among trees. Urticaceae, however, consist of exclusively herbs and shrubs, except for the Cecropiaceae genera *Cecropia* and *Coussapoa*, the only clear case of the evolution of trees from shrubby ancestors. All Celtidoids are trees, with the herbaceous Cannabaceae derived from it. There is no indication of trees being derived from herbs.

Leaf arrangement

See Fig. 2.6 B. Almost all species sampled have alternating leaves. There are some groups, however, that have an opposite leaf arrangement. Mapping the character states (alternate; opposite) on the phylogeny can show whether these groups are related or that the evolution of opposite leaves has occurred several times independently.

Within Rosales and the outgroup Fagales, the predominant, plesiomorphic leaf arrangement is alternating. Opposite leaves appear 6 times: in Elaeagnaceae (*Shepherdia*), Rhamnaceae (*Nesiota*), Barbeyaceae, Moraceae (*Streblus*), Urticaceae and the Celtidoid genus *Lozanella*.

Flowers

Within the traditional Ulmaceae s.l. flower sex differs for several genera. In the Rosales as a whole, flowers generally have both male and female organs (monoecious), but flowers bearing only male or female organs (dioecious), and flowers being either male or hermaphroditic (polygamous).

> "Flowers with both stamens and carpels precede those in which these occur
> on separate flowers" Bassey (1915).

We can confirm that the ancestral state for flower breeding system in the Rosales is monoecious. Dioecious flowers originate at least 8 times: in Rosaceae (*Aruncus*); Elaeagnaceae, Rhamnaceae

(*Berchemia* and *Barbeya*); Ulmaceae (*Hemiptelea*); Moraceae (*Maclura*); Urticaceae (*Myriocarpa*); the Celtidoid genus *Lozanella*; and the Cannabaceae. Flowers being polygamous only occur in Ulmaceae (*Holoptelea*) and *Celtis*.

Fruit type

Fruit type is a character for which the determination of the states (achene; drupe; syncarp; follicle; samara; capsule; winged drupe) is relatively easy as there are no intermediate stages. Fruit types can be basically divided into dry fruits (achenes, follicles, capsules), drupes, a syncarp is an aggregate fruit which consists of many individual fruits from separate ovaries within a common receptacle. Winged fruit types can be either a winged achene (samara) or a winged drupe (as in *Pteroceltis*):

- Achene: dry, indehiscent fruit with one seed.
- Drupe: indehiscent fruit with one seed surrounded by a hard stone or pit.
- Follicle: dry, dehiscent fruit with many seeds from a single carpel.
- Capsule: dry, dehiscent fruit with many seeds from 2 or more carpels.

The fruit type does not show a general trend throughout the Rosales, but for the families some patterns are worth mentioning: The Rosaceae is divided here into two clades; one with achenes (*Dryas*, *Geum*, *Potentilla,* and *Rosa*), and one with drupes, follicles, or fleshy fruits (*Crataegus*, *Aruncus*, *Prunus*). The phylogeny of the Rhamnaceae shows an evolution from drupes to capsules. As mentioned in the introduction, Ulmaceae can have either samaras (traditional Ulmoids) or drupes (traditional Celtidoids). Moraceae consist mainly of species with syncarpous fruits, with evolution to fleshy fruits (*Castilla*, *Brosimum*, *Broussonetia*), or drupes (*Dorstenia*, *Streblus*). The Urticaceae are all bearing achenes, except for the ex-Cecropiaceae genus *Coussapoa* (drupaceous). The Celtidoids all have drupaceous fruits; only the monotypic genus Pteroceltis has a winged drupe. This might be an adaptation of this species to its dry, temperate habitat in North-West China. The Cannabaceae show an evolution from the Celtidoid drupe to an achene.

Leaf margin

See Fig. 2.6 C. For the leaf margin, we looked at mature branches only, because juvenile leaves or leaves on water shoots can be morphologically very deviant. Three character states were scored: lobed, entire and serrate; serrate was scored when 1/3 or more of the leaf margin has serration.

For the leaf margin there are a few patterns noteworthy: In the Fagales and the Rosales not belonging to the former Urticales, a serrate leaf margin seems to be the ancestral state with evolution to entire margins occurring in all lineages; in the Rhamnaceae this pattern is the same as for the fruit type. The Ulmaceae can be divided into two clades, with the entire margined *Ampelocera* and *Holoptelea* being sister to all other serrate margined representatives. The Celtidoids also have predominantly serrate leaf margins, with entire leaf margins occurring in some specific clades: the genera *Aphananthe*, *Chaetachme*, and some African *Celtis* species. Lobed leaf margins occur only in *Morus, Cecropia* and the Cannabaceae.

Pollen

See Fig. 2.6 D. One of the most obvious characters for pollen is the number of pores; ranging from 2 - 5. Because many species can have either 4 or 5 pores, the character states were divided as follows: less than three pores, 3 pores, or more than three pores (<3 porate; 3 porate; > 3 porate).

The basic pollen type is 3 porate, which is not surprising given the current re-circumscription of the Eudicots into Tricolpates. Nevertheless there are some deviations: The Ulmaceae have more than 3 pores, a trait also occurring in *Hippophae, Berchemia*, *Dorstenia* and some representatives of the Urticaceae. A reduction of the number of pores can be seen in the ex-Cecropiaceae genera *Coussapoa* and *Cecropia* (Urticaceae), and the Celtidoid genus *Trema.*

Figure 2.6 A-D. Evolutionary trends of selected morphological characters traced over the parsimony jackknife majority-rule consensus tree, based on 134 taxa, with parsimony as the ancestral state reconstruction method. Terminals are coloured according to the genus (Celtidoids)., family (other Rosales)., or order (Fagales). Node labels indicate the main clades within the Urticalean Rosids: Cannabaceae (Can)., *Celtis* (C), *Chaetachme* & *Pteroceltis* (Ch), *Trema* & *Parasponia* (T+P), *Gironniera* (G), *Lozanella* (L), *Aphananthe* (A), Urticaceae & Cecropiaceae (Urt)., Moraceae (Mor), and Ulmaceae (U).
A Habit; B Leaf arrangement; C Leaf margin; D Pollen.

Fig. 2.6 A. Habit.

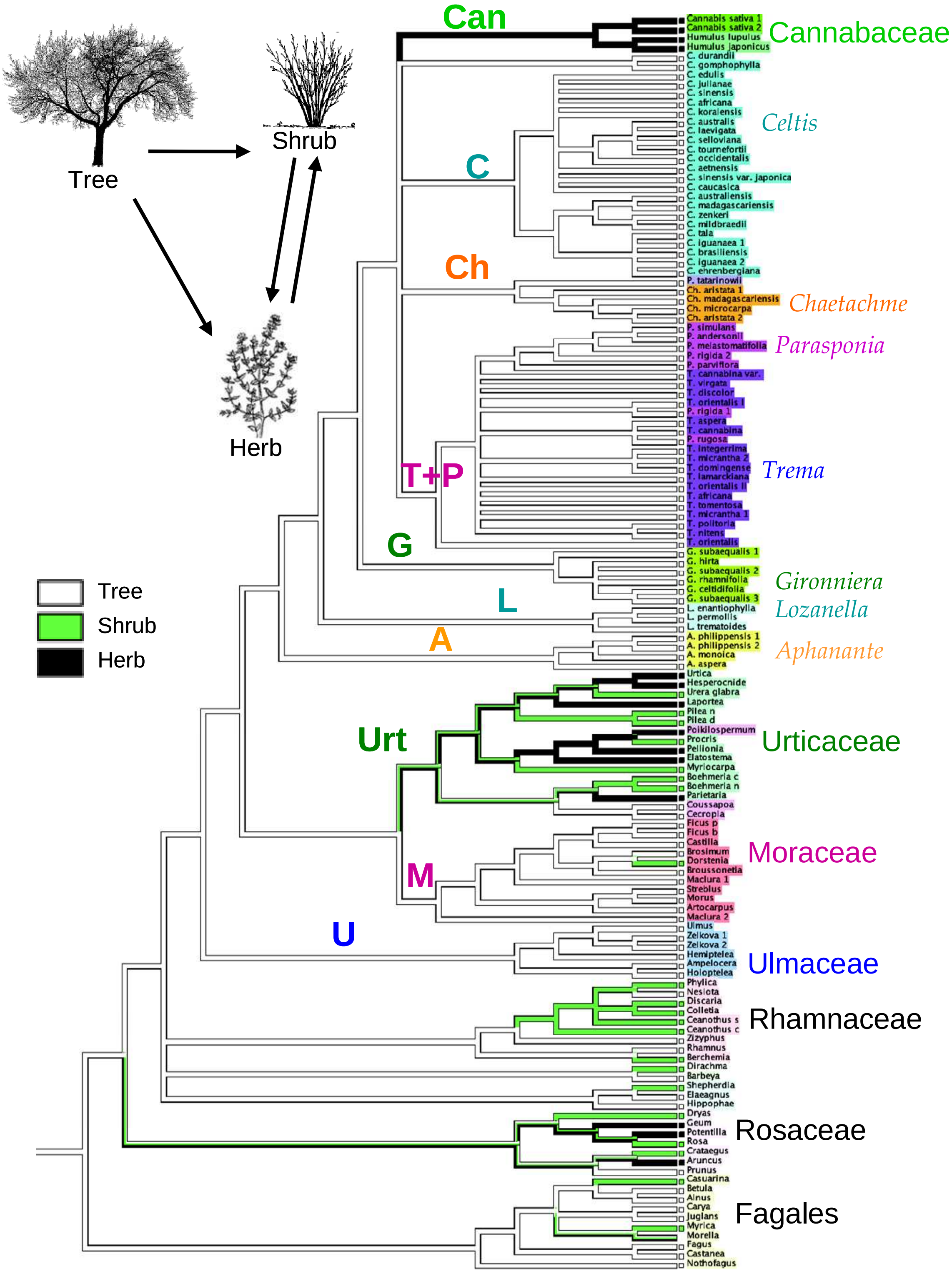


Fig. 2.6 B. Leaf arrangement.

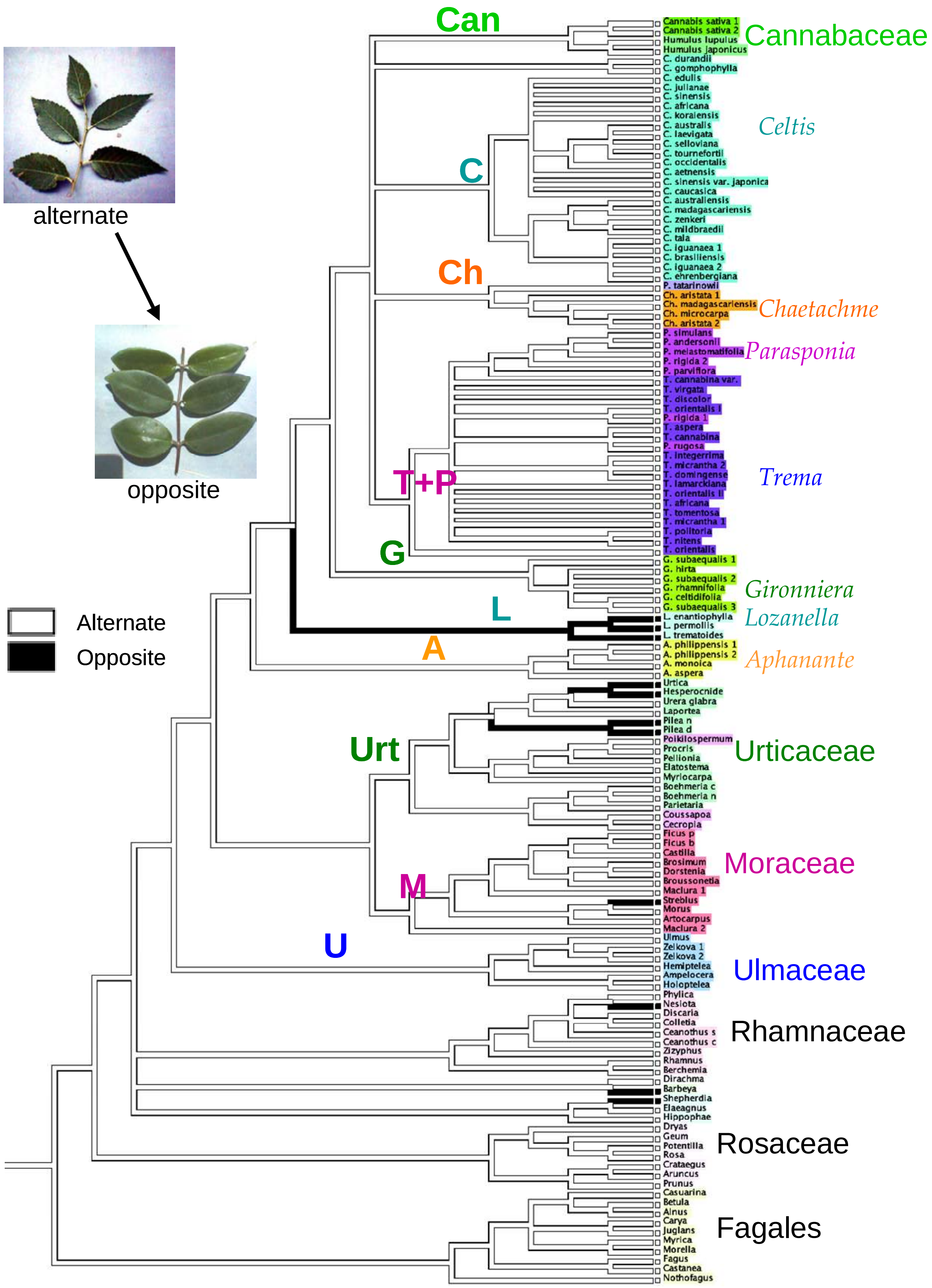


Figure 2.6 C. Leaf margin.

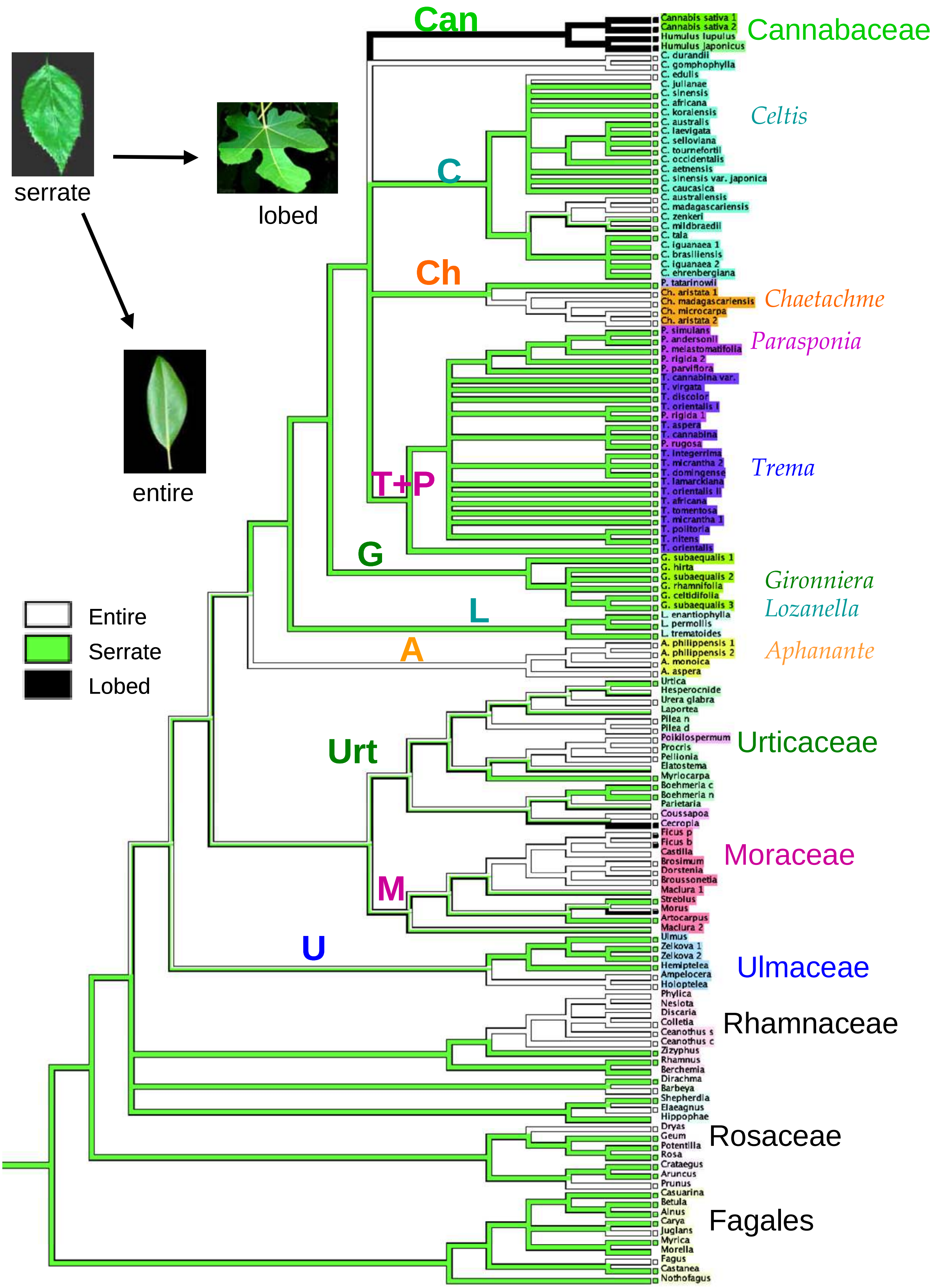
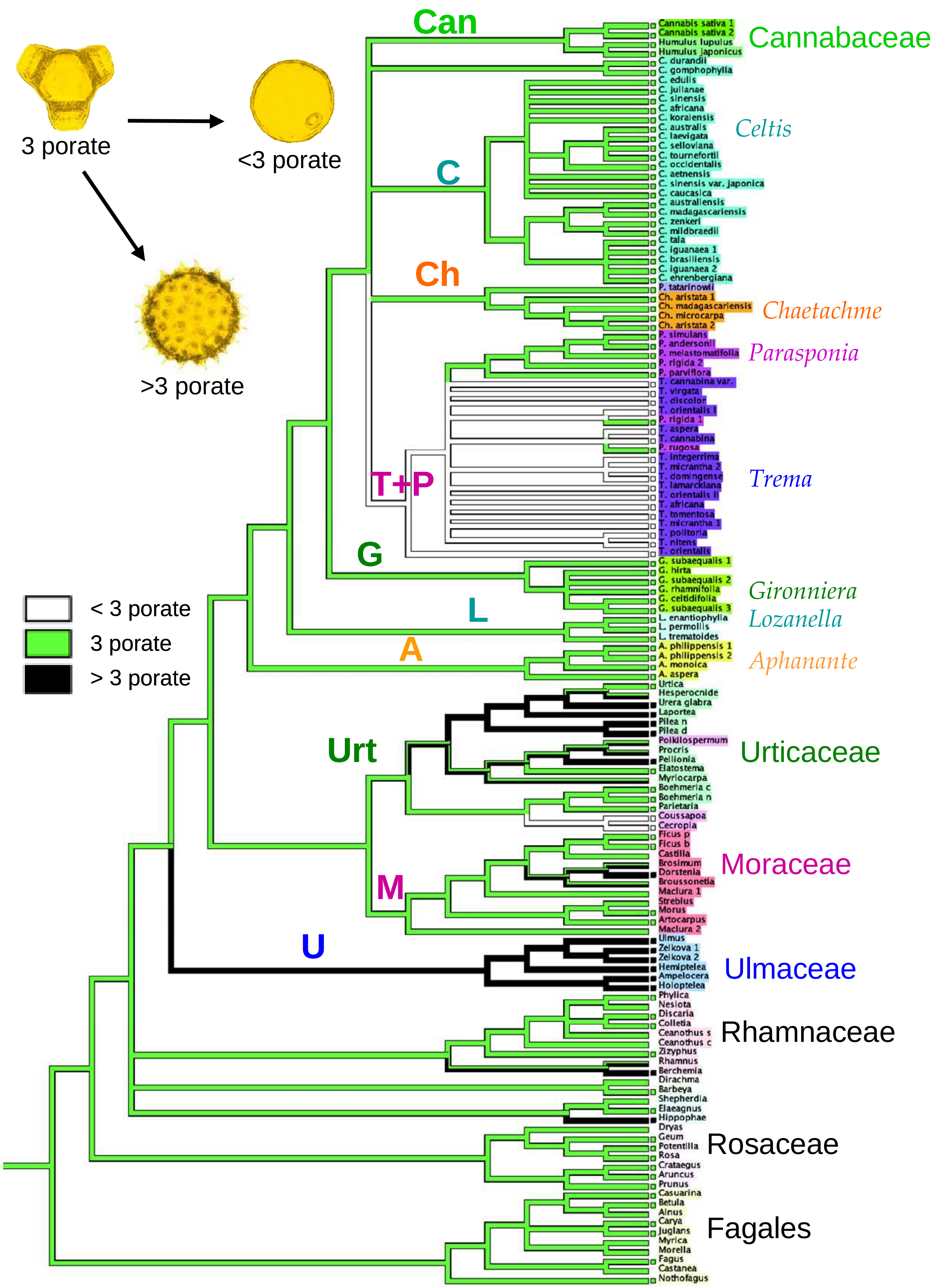


Fig. 2.6 D. Pollen.



Thorns and spines

Thorns and spines are two distinct morphological characters: the former are modifications of the stem, while the latter are leaf modifications. Thorns and spines are not common in the Rosales: within our taxon set they are confined to the Eleagnaceae, some groups in the Celtidaceae, and species of Ulmaceae (*Hemiptelea*) and Rosaceae (*Rosa*).

When plotting the character states (thorns; spines; absent) on the phylogenetic tree, it appears that in the Celtidoids some clades can be characterised by their thorns: The genus *Chaetachme* is bearing thorns, as is the *Celtis* subgenus *Mertensia* from the Neotropics. The evolutionary relationships between Eleagnaceae and the Ulmaceae are not resolved.

2.4 Phylogeny

Are the Celtidoids sister to a clade with Moraceae and Urticaceae as hypothesised by Sytsma et al. in 2002?

Our results clearly confirm that the Ulmaceae s.l. is not a monophyletic group, and that the Celtidoids must be separated from it. Ulmaceae s.s. is sister to the other Urticalean Rosids (Fig. 2.4). All 125700 MP trees have the Celtidoids s.l. as sister to a clade with Moraceae and Urticaceae. Although jackknife support for this relationship is only moderate (72% jackknife support, fig. 2.4) the high p.p values (97 and 99) (fig 2.5) in the Bayesian analyses and the congruence with the results of Sytsma et al. (2002) who acquired better support for this relationships with the addition of the chloroplast gene ndhF, indicate that support will probably increase with the addition of more character data.

Are the Celtidoid genera monophyletic?

Most Celtidoid genera are monophyletic; only the status of *Trema*, *Parasponia* and *Celtis* remains uncertain (Fig. 2.4). It is clear that not all genera are represented by all their species, and the addition of more taxa could alter this conclusion. But as our taxonomic sampling is relatively high already, we are confident that our conclusions will hold.

What are the intergeneric relationships within the Celtidoids?

Aphananthe is sister to all other Celtidoid s.l. genera. *Lozanella* appears as sister to the remainder, and *Gironniera* as sister to a clade comprising *Celtis, Chaetachme, Parasponia, Pteroceltis,* and *Trema*, but these relationships are not well supported. It is possible that when more data is added, the positions of *Lozanella* and *Gironniera* will switch, or that both will appear as sister to each other (Fig. 2.4).

What is the phylogenetic position of the Cannabaceae?

Cannabaceae are monophyletic and closely related to *Celtis*, *Chaetachme*, *Parasponia, Pteroceltis*, and *Trema*. *Chaetachme* does not have the derived base chromosome number x = 10 which characterises Cannabaceae and the other genera mentioned above (Sytsma et al. 2002), but because *Pteroceltis* (x = 10) is its sister lineage (fig 2.4), the possibility that the *Chaetachme*+*Pteroceltis* clade is sister to Cannabaceae cannot be excluded. The fact that the problematic line within *Celtis* tends to group with the Cannabaceae in the Bayesian analyses may be an indication that *Celtis* is the closest relative to the Cannabaceae.

2.5 Evolutionary trends

We feel that the taxonomic sampling used is actually insufficient for properly assessing the morphological trends in this clade. As this is a phylogeny of the whole order Rosales, it is sure that we missed some taxa having traits that would alter our conclusions about the trends, such as *Dendrocnide excelsa*, an Urticaceous tree of up to 40 m. Therefore, this part of our study should rather be regarded as an exercise than as a valid analysis.

Nevertheless, it is surprising to see that the two dicta of Bessey that were tested could actually be confirmed. This reaffirms the fact that, although molecular phylogenetics has brought about many changes in the classification of the Angiosperms, a large part of the traditional classification is still valid today. In our study, the delimitation of the Urticales and the evolutionary trends, both already described by Bessey in 1915 are corroborated.

2.6 Remaining questions and recommendations

The majority of research questions have been answered at least in part, but some questions about the phylogeny of the Celtdoids remain:

Do the genera *Celtis*, *Trema* and *Parasponia* represent monophyletic groups?
What are the closest relatives of the Cannabaceae? (and of *Celtis*?).
The phylogenetic results of the resolved part of the genus *Celtis* have generated a new question about the relation between phylogeny and biogeography of the genus (see Chapter 3).

Are African and Neotropical *Celtis* species sisters, or are the Neotropical ones derived from within the African taxa?
To be able to answer these phylogenetic questions about the Celtidoids, the most important thing is to add more character data. For the question regarding *Celtis*, enlarging the taxon set might also be beneficial: As *Celtis* is a very large genus, the addition of more *Celtis* species might provide a more solid basis for phylogenetic hypothesis about its intrageneric relationships. In order to be able to confidently make statements about the biogeography it is necessary to include Neotropical species not belonging to the subgenus *Mertensia*.

2.7 Conclusions

We can conclude that this study has generated many hypotheses about the phylogeny of the Rosales in general and the Celtidoids in particular. For a definitive elucidation of the evolution of the Celtidoids and the Cannabaceae, a follow-up study including more characters is necessary. The addition of a nuclear marker would be recommended to see if the chloroplast and nuclear genotypes contain any conflicting signal, which might suggest reticulate evolution. There is no doubt that such a follow-up study will generate many new evolutionary hypotheses about this highly interesting group of plants.

Chapter 3

PHYLOGENETIC RELATIONSHIPS OF AFRICAN *CELTIS* (CELTIDACEAE)

A. SATTARIAN; & L. J. G. VAN DER MAESEN

Summary

Celtis L. (Celtidaceae, formerly Ulmaceae-Celtideae), one of the smaller tree genera in Africa, comprises mostly evergreen trees, some of which are widespread and abundant. *Celtis* as a whole contains mostly trees, and are found in tropical and temperate regions of the world (Africa, Asia, South America, North America). *Celtis* was represented by c. 8 species in tropical Africa (Letouzey 1972) but in current research (this thesis) 12 species are recognized in Africa (Sattarian et al. 2005). The phylogeny of the genus was tested to see whether or not African *Celtis* are a monophyletic group within Celtidaceae. What are the relationships between the biogeographical distribution patterns in *Celtis*?

We used plastid *TrnL-F* DNA sequence data and morphology data for this study. We sampled a total number of 69 accessions, which we consider to cover 49 species of *Celtis*, 11 other Celtidaceae genera and nine outgroups, (see appendix 1 for details). For *Celtis* the sampling was based on the entire geographical distribution. We used Parsimony and Bayesian analyses. The topology of the jackknife tree has shown a clade of *Celtis* with 83% jackknife support (*trnL-F*, morphology) and without input of morphology this clade received 64% support. Generally, *Celtis* appears in an unresolved clade containing *Pteroceltis*, *Trema*, *Chaetachme*, *Humulus* and *Cannabis* (99%). The *C. gomphophylla* clade is sister to the African and Asian *Celtis*, however, the position of this clade is dependent on whether model-based analysis is performed or not.

3.1 Introduction

In this chapter we will focus on phylogenetic relationships in this widespread genus, and discuss various scenarios of its phylogeny and biogeography. We will first briefly review the taxonomy, ecology and biogeography of *Celtis* in general.

The taxonomic history of *Celtis* in general and especially African *Celtis* is treated in chapters 1 & 7 of this thesis. *Celtis* is part of the angiosperm family Celtidaceae Link which was previously considered to be part of Ulmaceae Mirbel (formerly Ulmaceae-Celtideae, see Table 1.1, this thesis.) (Elias 1970; Grudzinskaya 1967; Judd et al. 1994; Omori & Terabayashi 1991, 1993; Ueda et al. 1997; Song et al. 2001; see further Van Velzen, chapter 2 of this thesis, 2006). Celtidaceae Link now comprises ca. 100-150 species classified in nine genera (Todzia 1989; Grudzinskaya 1967; Sweitzer 1971; Soepadmo 1977; Ulloa 1995) that are widely distributed in different ecological habitats (e.g. temperate regions, savannah areas, rain forest).

The *Celtis* species, which are mostly trees, are found in all tropical, and many temperate regions of the world (Africa, Asia, South America, and North America). Some *Celtis* species of the family are ornamental; some are used for timber and reforestation. *Celtis* is a rather small genus in Africa comprising mostly evergreen trees, some of which are widespread and abundant, and some have a more restricted distribution (see below & chapters 1, 4, 5, 6, 7 of this thesis for more detail and examples of species characteristics).

Celtis species possess simple leaves that are of moderate size, usually leathery, often markedly asymmetrical at the base, acuminate, and mostly with parallel veins running between the nerves; petioles measure up to 12 mm long. The flowers are axillary on the current year's shoots, usually with male and hermaphrodite flowers, both kinds of flowers in the same inflorescence; fruits are drupes, varying from quite small to 20 mm in length. The endocarp is important to distinguish species of African *Celtis.* The endocarp shape varies from elliptic to ovoid, lenticular, or ovoid-beaked. The size of endocarp ranges from small (4 x 3 x 2 mm) to large (11 x 10 x 8) and is very useful in terms of identification of species. The endocarp shape varies from globular to polygonal. The outer layers of the endocarp differ (more detail in the chapters 6 in this thesis). There are main two types of outer layers of endocarp (smooth polygonal and rough polygonal) which may be related to dispersal. The endocarp colour varies from white, cream, and grey to brown. (More details in chapters 4 & 7 in this thesis).

3.2 Ecology of *Celtis* L.

In the flora of Africa, Celtidaceae Link (see Table 1.1, this thesis.) is a small family with as main genus *Celtis*, earlier known to be represented by c. 8 tree species (Letouzey 1972), but in current research 12 species are recognized (Sattarian & van der Maesen 2005). The distribution of African *Celtis* species ranges from North Africa (Algeria, Libya and Morocco) to South Africa and Madagascar. Several species are found in rain forest (*Celtis tessmanii, C. mildbraedii)* (Letouzey 1972; Keay 1989) or in semi-deciduous forest (*Celtis adolfi-friderici*, *C. prantlii*, *C. zenkeri*). Other *Celtis* are shrubs or small trees of rain forest undergrowth (*C. gomphophylla*), or found on the forest/savannah boundary, or sometimes in mountain forest (*C. africana*). *Celtis toka* is a fairly large tree with a compact crown, growing beside streams or planted in villages in the Sudano-Sahelian zone (Flora of Tropical East Africa 1966). The drupaceous fruits of *Celtis* vary in colour from bright yellow to orange, deep red, and purple and are primarily bird-dispersed (Berg & Dahlberg 2001 & pers. obs. in Wageningen Botanical Garden, 2002). *Celtis philippensis* var. *wightii*, which grows in coastal forests in Malesia, has been suggested to be water-dispersed (Soepadmo 1977).

In South Asia, especially in Malesia, species of *Celtis* may be classified in two rather distinct ecological groups. The first group is informally named here the '*Celtis philippensis*' group, containing *C. philippensis*, *C. hildebrandii*, C. *latifolia*, *C. luzonica*, *C. paniculata*, and *C. rigescens*, These species are found mainly in lowland forest, both primary and secondary, and are an important constituent of the understorey tree community in moist areas. The second group, the '*Celtis tetrandra* group', includes C. *rubrovenia, C. timorensis*, and *C. philippensis* var. *wightii*, and is confined to areas with a rather pronounced seasonal climate, or they occur in wetter regions, they grow on strongly drained substrates, e.g. rocky shores, and limestone. In tune with this environmental preference, the '*C. tetrandra* group' group shows a more prominent flush-wise growth habit and its species are completely or partly deciduous (Soepadmo 1977). In Africa there are also three main habitats for *Celtis*: rain forest which contains *Celtis adolfi-friderici* and *C. tessmannii*, dry Mediterranean habitat with *Celtis australis*, and savannah areas in which *Celtis prantlii*, *C. africana*, *C. toka*, *C. gomphophylla* are found (Sattarian et al. this thesis 2006). In S. America most *Celtis* grow at forest edges. Globally *Celtis* grows nowhere at higher altitudes than 1000-1500 m.

3.3 Biogeography of *Celtis* L.

"Biogeography studies the patterns of spatial variation in organism distributions and examines characteristics that constitute their geographical range" (Crisci 2001). Biogeography includes the classical subject areas geography, geology and biology. There are two main traditional research lines in biogeography: ecological biogeography and historical biogeography (Humphries 2000 ; Crisci 2001; Myers & Giller 1988).

Extinction, dispersal and vicariance are the main processes in the distribution of organisms, there is not any difference in opinion about extinction, because it is a death of organisms or populations, but other processes (dispersal, vicariance) have been discussed differently. The centre of these discussions concerns disjunct distribution patterns, many biogeographers attempted to explain how the common ancestor originally occurred in the one area and later dispersal into another area and which processes affect distribution (Hill & Jordan 1993; Linder & Crisp 1995).

In the dispersal viewpoint, the ancestral population was limited by existing barriers, and if it moved into new areas, colonizing there and remaining isolated from the original area, they may differentiate into new taxa. But in the vicariance viewpoint the ancestral population is divided by the development of barriers, and barriers cause disjunction (Crisci 2001).

Dispersal was used for a long time as important explanation for distribution of organisms. Cain (1944) and Croizat (1958) discussed the dispersal explanation as the main process in biogeography and later on developed vicariance as equally important (Crisci 2001).

According to Croizat (1964) and Craw et al. (1999) “the vicariance-dispersal opposition can be resolved by applying a biogeographic model (the vicariance form-making or periodic mobilism) involving alternating cycles of dispersal and vicariance. This solution recognizes both dispersal and vicariance as important processes by which organisms achieve their geographical distributions” (Crisci 2001).

Before the 1960s, oceanic dispersal was a dominant theory for distribution, later on especially during the 1960s and 1970s, two development ideas changed in biogeography, the first one was validation of the plate-tectonic theories which supported vicariance explanations, the second one was the spread of cladistic thinking which produced a method for reconstructing phylogenetic relationships. Combination of the plate tectonic and cladistic methods provided a good way to explain disjunct distributions (Crisci 2001; Patterson 1981). Over the last decades, understanding of plant molecular phylogeny and molecular dating has improved, enabling better testing of historical biogeographical hypotheses.

There have been many studies published over the last decade that test hypotheses on particular migration patterns and biogeography of plants (Renner et al. 2001(Melastomataceae); Lavin et al. 2003, 2004 (Fabaceae), Davis et al. 2002 (Malpighiaceae); Richardson et al. 2004 (Annonaceae & Rhamnaceae); Pennington 2004 (Annonaceae)). In the following paragraph we discuss some of these studies. In general, however, based on these molecular phylogenetic trees, evidence for intercontinental angiosperm dispersal is accumulating, only in old groups such as in Lauraceae (Chanderbali et al. 2001) and Annonaceae Gondwanan vicariance has been suggested.

Phylogenetic analyses of the Annonaceae and Rhamnaceae based on *rbcL* and *trnL-F* show that one explanation for the distribution pattern of African and South American taxa is vicariance (the Gondwanan break-up).The distribution of Rhamnaceae is influenced by Gondwanan break-up, e.g. the Ziziphoid group is cosmopolitan with a predominantly Southern Hemisphere distribution, and suggesting a possible Gondwanan origin; this distribution suggests that the whole southern group was widespread throughout Gondwanaland and parts of Laurasia before these continents broke up (Richardson et al. 2004). This explanation for biogeographic disjunction involving South America and Africa (vicariance of western Gondwana) is problematic because many groups of plants originated and diversified after the last known connection between Africa and South America (Davis et al. 2001) and vicariance resulting from the break-up of Western Gondwana cannot explain some of the disjunct angiosperm lineages (Richardson et al. 2004; Pennington et al. 2004).

A historical biogeography approach complementary to testing migratory pathways is the exploration of affiliations of taxa that have contributed to the composition of (oceanic or continental) island floras. Such an approach was followed by Galley & Linder (2006) focussing on affiliations in the model system the Cape Floristic Region. It shows that Cape clades have Australian rather than African relationships. The Cape flora has been assembled over a long time period, and received more contributions from Australia than from Africa (Galley & Linder 2006); also many Cape clades show a relationship with Eurasian temperate flora. There is no single geographical source of the distinctive Cape flora and Cape clades share a common time of differentiation from geographical neighbours (Galley & Linder 2006).

Phylogeny based on chloroplast genes (*ndhF)* and nuclear phytochrome C (*PHYC*) (Davis et al. 2002) shows that Malpighiaceae originated and began to diversify in northern South America in the early Palaeocene, and from South America, different wing-fruited species may have migrated in North America via scattered continental or volcanic islands that connected North and South America, and from North America, these lineages could have migrated eastward across Laurasia into the Old World via connections across the North Atlantic, and then diversify in Africa and Madagascar and also in Asia. The North Atlantic Pathway is a way of the migration of several lineages of Malpighiaceae at different times (Davis et al. 2002).

Boreal tropical connections across the North Atlantic during the Eocene are evidence to understanding patterns of disjunction around the Northern Hemisphere especially between Eastern Asian and Eastern North American plants, and indicated an important pathway of global distribution for tropical groups (Sanderson 2001).

Molecular phylogeny, fossil dating and biogeography of both Annonaceae and Myristicaceae was studied involving *rbcL* gene analysis and morphology, this study converges on a fairly coherent story considering both plate tectonics and long-distance dispersal (Doyle et al. 2004)

Celtis is also one of the widespread genera in different continents (Sattarian et al. chapter 1, this thesis) and migration patterns of the this species would be interesting to be tested: which pathway played an important role in biogeography of *Celtis*: Gondwanan break-up, North Atlantic pathways, boreotropic, or the Antarctica route? Did migration of *Celtis* spp. occur from South America via scattered continental and volcanic islands that are connected to North and South America and then by the North Atlantic land bridge to the northern hemisphere and Africa as well or the other way around, because dispersal of the these species is done by birds and its fruits are quite attractive mostly for birds (Soepadmo 1977).

3.4 Taxonomy and phylogeny of *Celtis* L.

The major challenge in the taxonomy of *Celtis* has been the difficulty in finding proper morphological characters to distinguish species well. More than 500 published species epithets are enumerated in the International Plant Names Index (IPNI 2004), the most recent database listing *Celtis* on a worldwide basis. Because a world monograph is lacking, species concepts vary considerably among regional floras. Current trends have been toward recognizing fewer but more variable species. Although pragmatic, this approach precludes a deeper understanding of the systematic relationship among species or their evolution and biogeography. So, phylogenetic relationships at genus and species level within Celtidaceae Link are still poorly resolved (Sytsma et al. 2002; Song et al. 2001; Van Velzen, Chapter 2 in this thesis 2006; Chase 1993; Judd et al. 2002; Ueda et al 1997; Wiegrefe et al. 1998, Song et al. 2002).

The intergeneric relationships within the Celtidaceae Link based on *rbcL* and *trnL-F* lack significant support (Sytsma et al. 2002; Song et al. 2001; Van Velzen, Chapter 2 in this thesis 2006). *Aphananthe* is sister to all the Celtidaceae genera, *Lozanella* is also sister to remainder, and *Gironniera* is sister to a clade that comprises *Celtis*, *Chaetachme*, *Parasponia*, *Pteroceltis* and *Trema*, but these relationships are not supported well, and we still need to add more taxa to get better support (Sytsma et al. 2002; Song et al. 2001; Van Velzen, Chapter 2 in this thesis 2006). These studies generated some remaining questions like: do the genera *Celtis*, *Trema*, and *Parasponia* represent monophyletic groups? Which genera are close to Cannabaceae, what are the relationships between phylogeny and biogeography of *Celtis* (Van Velzen, Chapter 2 in this thesis 2006; Song et al. 2001).

In general, phylogeny data on African *Celtis* is lacking (Sytsma et al. 2002; Song et al. 2001; Van Velzen, unpubl. Chapter 2 in this thesis 2006; Chase 1993; Judd et al. 2002; Ueda et al. 1997; Wiegrefe et al. 1998, Song et al. 2002).

All published studies so far on *Celtis* were done at the level of the family in general and genera of the Celtidaceae, not in depth at species level. E.g. family phylogenies are based on evidence from floral anatomy (Chernik 1975, 1981), fruit morphology (Chernik 1980), seed coat anatomy (Chernik 1982), embryology, wood anatomy (Sweitzer 1971), pollen morphology (Zavada 1983; Takahashi 1989), leaf venation (Terabayashi 1991), and flavonoid chemistry (Bate-Smith and Richens 1973; Giannasi 1978). The Ulmoideae with their slightly larger hermaphroditic flowers and pollen, spiral perianth and stamen traces are considered to be more primitive than the Celtidoideae (Cronquist 1981, Leroy 1952; Hutchinson 1958; Soepadmo 1977). Advanced characters in the Celtidoideae include smaller flowers; fewer stamens, whorled perianth, and the absence of any vestigial stamen, permitting recognition of two sub-families. Many members of the Celtidoideae have a greater affinity to the Moraceae than to other Ulmaceae (Grudzinskaya 1967; Chernik 1975 1980, 1981, 1982; Takaso & Tobe 1990). Based on leaf venation and karyomorphology, within the Ulmoideae (Cronquist 1981) are distinguishable *Hemiptelea, Planera, Ulmus*, and *Zelkova* on the one hand and *Holoptelea* and *Phyllostylon* on the other (Oginuma et al. 1990). Within the Celtidoideae (Cronquist 1981; Leroy 1952; Hutchinson 1958; Soepadmo 1977), *Gironniera* may have an isolated position based on karyomorphology: n=14. (Oginuma et al.1990), the other genera have n=10 or 13. *Ampelocera* is distinct within the Celtidoideae in having a vernation pattern more like the Ulmoideae than the Celtidoideae, as well as having a distinctive flavonoid chemistry (Giannasi 1978), and pollen wall structure (Takahashi 1989). Morphologically and anatomically, *Aphananthe* and *Ampelocera* appear to bridge the Celtidoideae to the Ulmoideae (Manchester 1989). (more details in chapter 1 in this thesis).

In general, phylogeny data on African *Celtis* is lacking or only included in broader phylogenetic studies (Sytsma et al. 2002; Song et al. 2001; see also Chapter 2; Judd et al. 2002; Ueda et al. 1997; Wiegrefe et al. 1998, Song et al. 2002, Whittemore 2005: Islam, et al. only 2 posters at IBC Vienna, 2005) and studies on genetics of *Celtis* species are few (e.g. Whittamore et al. 2005). Therefore this project set out to fill some of the gaps in our knowledge, as well as addressed some of the remaining questions (Van Velzen, Chapter 2, in this thesis 2006) such as intergeneric relationships of Celtidaceae or relationships between phylogeny and biogeography.

So far, the phylogenetic results of the resolved part of the genus *Celtis* (Sytsma et al. 2002; Song et al. 2001; Ueda et al 1997; Wiegrefe et al. 1998; Song et al. 2002; see also Chapter 2) have generated questions about the relationships between phylogeny, morphology and biogeography (Judd et al. 2002), and these have been addressed in this thesis in Chapter 2 (Van Velzen et al.). We were able to answer part of the phylogenetic questions about *Celtis.* The important thing was to add more character data and taxa which could be beneficial to understanding of this genus, because *Celtis* is a large genus compared with the other genera in the Celtidaceae family and distribution is also very wide, so for this project we added all African *Celtis* as well as a few of the Asian, and South American *Celtis,* to get a proper understanding of the phylogeny of *Celtis.*

Morphologically, African *Celtis* are similar to the Asian *Celtis* and Australian species; both groups have no thorns. Berg (2001) classified the South American species in a sub-genus *Mertensia* (Berg 2001). The leaves and their venation differ between the continents. Ecologically, in Africa there are two species in rain forest (*Celtis tessmannii, C. adolfi-friderici*) and the other African *Celtis* occur in savannahs outside the forest, and one species is found in mountains of North Africa: *Celtis australis,* which is also present in Asian and South Europe as well.

Biogeography of *Celtis* also is an interesting area to understanding the pattern of the distribution: did the species migrate from South America to North America and Asia or the other way around. As stated above the phylogeny and morphology of the *Celtis* is lacking as well as addresses some of the remaining questions (Van Velzen, unpubl. Chapter 2 in this thesis 2006). Our study focussed on the following objectives:

1. Is African *Celtis* monophyletic within Celtidaceae?
2. What is the relationship between phylogeny and biogeography? Because *Celtis* is presented in different habitats in the world, it would be interesting to assess the relationship between phylogeny and habitat such as rain forest, savannah, and dry area (as in Schrire et al. 2003).
3. What is the relationship between phylogeny and morphology? African *Celtis* and Asian *Celtis* have more similarity morphologically, and South American *Celtis* having thorns are different from Asian and African *Celtis*, so we should understand the relationships between these two aspects.

3.5 Materials and Methods

In this study, the cpDNA region *trnL-F* and morphology have been used as a source of phylogenetic markers for reconstructing the phylogeny of African *Celtis*. The *trnL-F* consists mainly of two non-coding regions (the *trnL* intron and *trnL-F* intergeneric spacer). The succession of conserved *trn* genes and apparent absence of gene re-arrangements in the wider *trn T-F* region facilitated the design of plant universal primers by Taberlet et al. (1991), and since then the *trnL-F* region has become known as one of the most widely used chloroplast markers for phylogenetic analyses in plants (Quandt et al. 2004). The marker consists mainly of two non-coding regions (the *trnL* Group I intron and the *trnL-F* intergenic spacer (see Chapter 2, Fig. 2.2). It is relatively fast evolving and is consequently used in studies at the generic level (Hadiah 2003; Paul et al. 2005, Pirie 2005), as well as at the species level (Bakker et al. 2004).

In addition to the DNA sequence data we also included morphology data in our phylogenetic analysis. The morphological characters were based on the studies in this thesis, from herbarium specimens and information from Floras (chapters 4, 5, 6 and 7 in this thesis). We selected 10 characters (table 3.1): we included some of the characters which are very conspicuous; there is no overlap between characters and they can split into character states, because the main and important parts of the characters concern the definition of quantitative characters states. This proves to be especially problematic when such characters cannot be split into character states on the basis of discontinuities in morphometric space, i.e. gaps (Schuh 2000; Pelser et al. 2004). We selected 10 characters which are not overlapping and have no intermediate states. All the 10 characters were coded as binary or multistate characters and were treated as unordered in the phylogenetic analyses.

3.5.1 Taxon sampling

We sampled a total number of 69 accessions, covering 49 species of *Celtis*, 11 from other Celtidaceae genera and nine outgroups (see appendix 3 for details). For *Celtis* the sampling was based on worldwide geographical distribution, using herbarium specimens and silica-dried leaves sampled from Africa (14), South America (10), and Asia (12), this means that we have reached 50-81% of complete taxonomic sampling, depending of the number of species recognized in the genus. Additional gene sequences used in this study were used from current research (van Velzen et al. this thesis Chapter 2) and Gen Bank (13 accessions).

Trema, Ulmus, Cecropia, Ficus, Dirachma, Zelkova, Barbeya and Humulus were included as outgroups based on studies on Celtidaceae that indicated genera of Celtidaceae that have a close relationships with Cannabaceae, Moraceae and Urticaeae rather than with the Ulmaceae s.s. (Sytsma et al. 1996; Zavada et al. 1996; Ueda et al. 1997; Wiegrefe et al. 1998). Appendix 3 presents a list of taxon sampling.

Table 3.1. Morphological characters and coding.

Characters	**Character States**			
Life cycle	Herb (1)	Shrub (2)	Tree (3)	
Leaf	Simple (1)	Compound (2)		
Leaf margin	Entire (1)	Serrate (2)	Lobed (3)	
Leaf arrangement	Alternate (1)	Opposite (2)		
Venation	3 veins at base (1)	Pinnate (2)		
Indumentum	Smooth (1)	Rough (2)		
Pollen shape	≥ 3-porate (1)	≤ 3-porate (2)		
Fruit type	Drupe (1)	Nutlike (2)	Syncarp (3)	Samara (4)
Seed wing	Absent (0)	Present (1)		
Thorn	Absent (0)	Present (1)		

3.5.2 DNA extraction and PCR amplification

Total genomic DNA was extracted from herbarium or silica-dried leaves (10-25 mg) using a modification of the CTAB extraction protocol of Doyle (1987), following the DNA extraction protocol of the Wageningen Biosystematics Group (Vrielink et al. 2005). Concentration and quality of the extracted DNA was measured by using the Nanodrop ND-1000 spectrophotometer. Amplification has been performed in a volume of 50µL containing 37-123 ng genomic DNA, 0.2 µM of each primer and dNTP, 3 mM Mgcl 2, 75mM Tris-HCL, 20mM(NH4)2SO4, 0.01% Tween 20, and 1.5 unit Taq polymerase. The trnL-F region is amplified in one part using primers c and f or in two parts using primer combinations c-d and e-f (Taberlet et al. (1991). The PCR profile was 1 min. denaturation at 94°C, 1 min. annealing at 53°C, 2 min. extension at 72°C, followed by one cycle of 7 min. at 72°C (Taberlet et al. 1991). After visual inspection on a 1%-agarose gel, fragments are cleaned using Qiaquick purification (Qiagen) following the manufacturer’s protocol and eluted in 25µL MQ water.

The cleaned fragments were sequenced using a fluorescent dye-labeled sequencing reaction (DYEnamic tm ET Terminator Cycle Sequencing Kit, Amersham Biosciences), and high-throughput ABl sequencing facilites at Greenomics, Wageningen UR.

3.5.3 Sequence analysis

Sequences were assembled and edited using Staden version 1.5.3. (http://Staden.sourceforge.net/). In case of disagreement with two tracers, these polymorphic sites were resolved unambiguously. When all editing had been done, and we felt that all consensus sequences represent tracers in the best possible way, we saved the consensus sequences in the FASTA format.

Automatic alignment of sequences was carried out using Clustal-W as implemented in Bio-Edit (Hall 1999), for further alignment by eye we used the same software, and MacClade version 4.07 (PPC). Nine indels in the final alignment were coded as present/absent characters where they could be coded unambiguously, following the simple indel coding protocol as described by Simmons & Ochoterena (2000). The ten morphological characters described above (see table 3) were also included in the matrix.

3.5.4 Phylogenetic analysis

We choose to analyse our data using both a parsimony- and a model-based approach. In general, the parsimony approach for inferring phylogeny operates by selecting trees that minimize the total tree length, the number of evolutionary steps (transformations from one character state to another) required to explain a given set of data (e.g. Steel & Penny 2000; Felsenstein 2004 p. 97; Holder & Lewis 2003). Parsimony is a criterion that minimises assumptions, which implies that MP favours the tree that require the fewest evolutionary changes to explain the observed data (Hennig 1963;

Farris et al. 1982: Steel 2000; Whelan 2001; Felsenstein 2004). In parsimony, the score is simply the minimum number of substitutions or ‘character state changes’ that could possibly produce the data. The advantages of the parsimony approach are that it is fast enough for the analysis of hundreds of sequences, and robust if branches are short (Holder & Lewis 2003).

However, if there are great differences in the rates of character evolution between lineages such that some lineages are evolving very rapidly, and if the pattern of variation is sufficiently constrained (i.e., only a limited number of character state exist), then unusually long branches are often connected to each other whether or not they are actually closely related. This phenomenon occurs because numerous random changes, some of which appear in parallel in the two lineages, outnumber the information that shows common ancestry. The problem cannot be circumvented by acquisition of more characters, these merely add to the number of parallelisms linking the two rapidly evolving (Judd et al. 2002). This situation is called long branch attraction or the Felsenstein zone and can affect all methods of tree construction (Judd et al. 2005; Wiens 2005; Bergsten 2005).

“The parsimony analysis has a few obvious disadvantages such as the score of a tree which is completely determined by the minimum number of substitutions among all the reconstructions of ancestral sequences. Another serious drawback of parsimony arises, because it fails to account for the fact that the number of changes is unlikely to be equal on all branches in the tree. When calculating the parsimony score of a tree, a mutation counts as one demerit to the score no matter where it occurs. Nucleotides that are present at the ends of long branches might be similar because of convergent evolution rather than direct inheritance, and parsimony does not allow for convergence along long branches as an explanation of similarity. This property makes parsimony susceptible to long-branch attraction, in which two long branches that are not adjacent on the true tree is inferred to be the closet relatives of each other by parsimony” (Holder & Lewis 2003).

Maximum likelihood (ML) is another optimality criterion which is a more statistical approach to phylogeny reconstruction (Whelan et al. 2001). Edwards & Cavalli-Sforza (1964) wanted to apply a ML criterion to phylogeny reconstruction. The ML estimate of phylogeny is the tree for which the observed data are most probable. The likelihood of the observed sequences depends on an explicit model of the process of DNA substitution and tree (Felsenstein 1984). One of the disadvantages of the ML is adoption of the model that may not describe the true evolutionary process of characters (Sober 2004).

Bayesian analysis, is based on an 18th century theorem by the reverend Thomas Bayes (see http://www.bayesian.org/bayesian/bayes.html) (Huelsenbeck et al. 2002), and is a widely applied statistical tool outside systematics. Three groups of researchers independently proposed using Bayesian inference of phylogeny: Yang & Ranala (1996), Mau (1996) and Li (1996); and this approach has become common nowadays (Rendle et al. 2005). Bayesian inference of phylogeny is based on a quantity called posterior probability of a tree, or in other words it is a branch of statistics that focuses on the posterior probability of hypotheses. The posterior probability is proportional to the product of the prior probability and the likelihood (Holder & Lewis 2003). This analysis also has advantage of strong connection to the maximum likelihood method, it might be a faster way to assess support for trees and it also has disadvantages of the prior distribution for parameters which must be specified (Rendle et al. 2005). Data were analysed using PAUP* version 4.0b10 for Macintosh, on a Macintosh G5 and Mr Bayes version 3.1.1.

3.5.5 Parsimony analyses

We used jackknife support analysis with heuristic search, the number of jackknife replicates being 1000, the nominal percentage of characters deleted in each replicate was 37, 1248 characters. All the characters were of unordered type, all characters had equal weight. Gaps were treated as missing, and the addition sequence was random. The number of replicates was 10; the number of trees held at each step during stepwise addition was 1. Branch-swapping algorithm tree was (tree bisection-reconnection (TBR).

3.5.6 Bayesian analysis

Bayesian analysis was initially conducted using default settings. When there was not sufficient mixing of the MCMC chains it meant that the default temperature for the heated chains (T=0.20) was too high (Ronquist & Huelsenbeck 2004); these rates can be adjusted after some analyses. Therefore, normally some pre-run should be made and the proposed parameters and temperatures have to be adjusted. For our analysis the temperature was set to T=0.05. By this temperature, the Bayesian MCMC chains performed better. Default prior values for DNA substitution models were applied to each partition.

Further details of settings were as follows: 70 taxa, character-set ‘non-coding’ = 1-1239, character-set ‘standard morphology’ = 1240-1248, partition region = 2: non_coding, coding, ratepr = variable, set partition region, 1st apply to= (1) nst=6 rate = invgamma, 1st applyto = (2) coding = informative, unlink statefre = (all), revmat = (all), shap = (all), pinvar = (all), mcmcp ngen = 4000000, nchains = 4, printfreq = 100, samplefreq = 100, TBR+I+G, T = 0.05, analyses were run for 4,000,000 generations with for simultaneous MCMC chains to calculate posterior probabilities (PP) and one tree per 100 generations was saved. The burn-in values were determined empirically from the likelihood values and 50% majority rule-consensus trees calculated together with approximations of the PP for the observed bipartitions.

3.6 Results

3.6.1 Maximum Parsimony

The *trnL-F* region had an aligned length of 1248 characters. The *trnL-F* region with the indel characters contained 225 parsimony informative characters (15.7%). The jackknife majority rule consensus tree based on *trnL* and indels had 32 nodes. The MP search resulted in a single tree of 734 steps, CI = 0.725, RI = 0.858. The multiple morphological characters provided another 9 characters and in this case the number of parsimony informative characters was 249 (19%), The jackknife majority-rule consensus tree was better resolved special value supports and has 34 nodes, and tree length is 692 steps, CI=0.750, RI=0.862 (Figs 3.1 & 3.2). but this difference is not significant.

The jackknife topology shows a clade of *Celtis* with 83% jack support (*trnL-F* and morphology data), and without morphology this clade received (64%) value support (fig. 3.1, 3.2 and 3.2). Generally *Celtis* appears in an unresolved clade containing *Pteroceltis*, *Trema*, *Chaetachme*, *Humulus* and *Cannabis* (99%). This clade is sister to *Gironniera* (67%), then to *Lozanella* (99%) and to *Aphananthe* (59%). and the clade containing all Celtidaceae and Cannabaceae is related to *Ficus*, *Brosimimum*, *Morus*, *Cecropia*, *Pellionia* (100%) and finally sister to *Ampelocera*, and *Ulmus* (100%).In general this topology shows that genera of Celtidaceae are monophyletic. In the *Celtis* clade *Celtis gomphophylla/durandii* is sister to all other *Celtis*. South American taxa form a clade supported with 81% jack in this topology.

The clade comprising *Celtis gomphophylla* is sister to the rest of the *Celtis* (African and Asian and South American species; and also to the South American clade, The clade which contains *Celtis africana* and *C. toka* is nested to the African and Asian species and only the South American taxa included are clearly monophyletic (81% jack), but in the clade of South American taxa polytomy can be seen. African taxa occur at three unrelated lineages, intermixed with the Asian taxa. The two African *Celtis* clades contain *Celtis gomphophylla* and allies, and *Celtis zenkeri* and allies, respectively, wheras *C. tessmannii*, *C. toka*, *C. africana* and *C. malagasica* are part of an Asian assemblage. Generally African species are more resolved than Asian species. Obviously, for better-resolved patterns more and perhaps different markers are needed as well as more taxa.

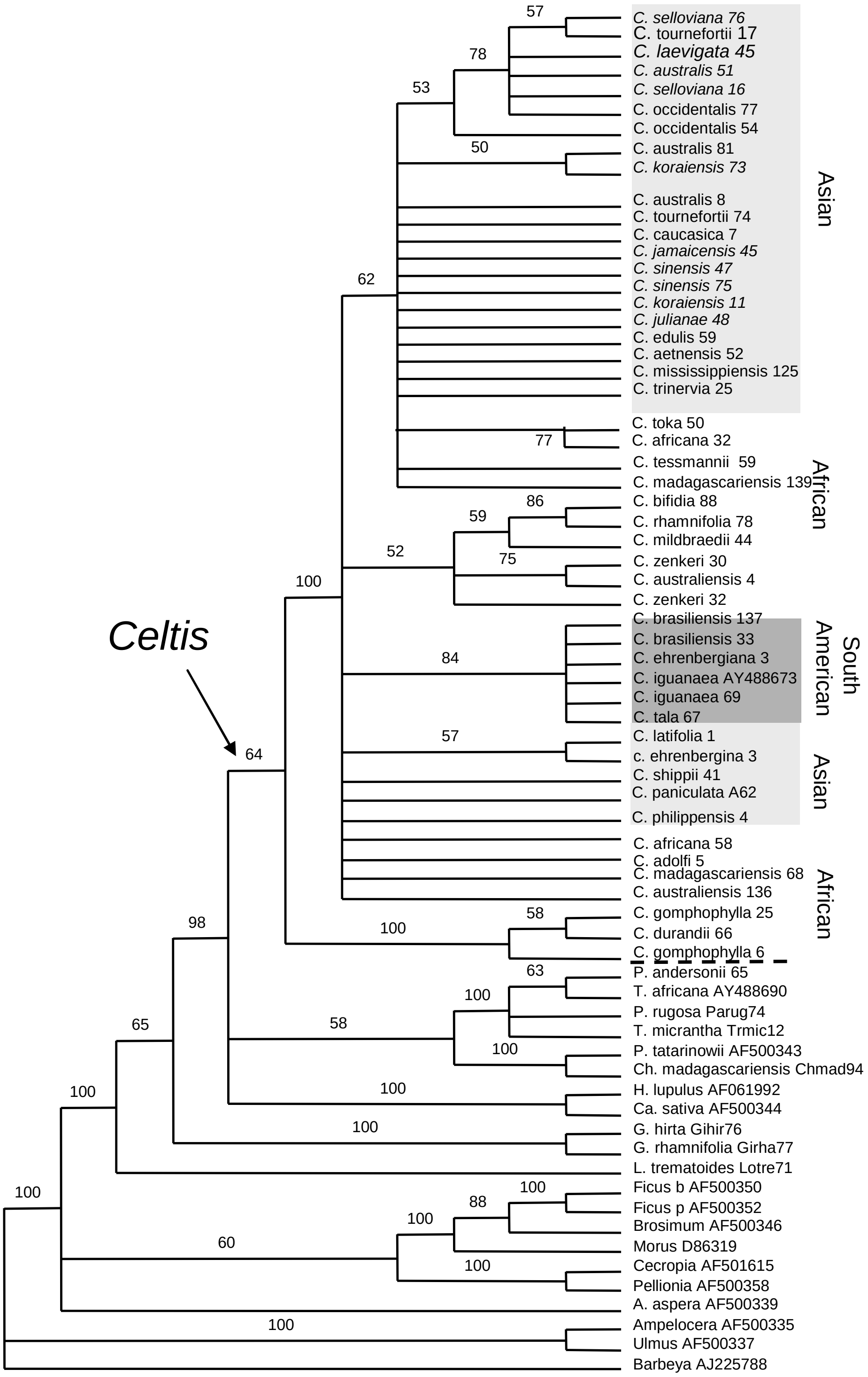


Figure 3.1. Parsimony jackknife-majority-rule consensus tree (1000 replicates, TBR swapping). Support values > 50% are shown, based on *trnL-F* (cpDNA) and indels.

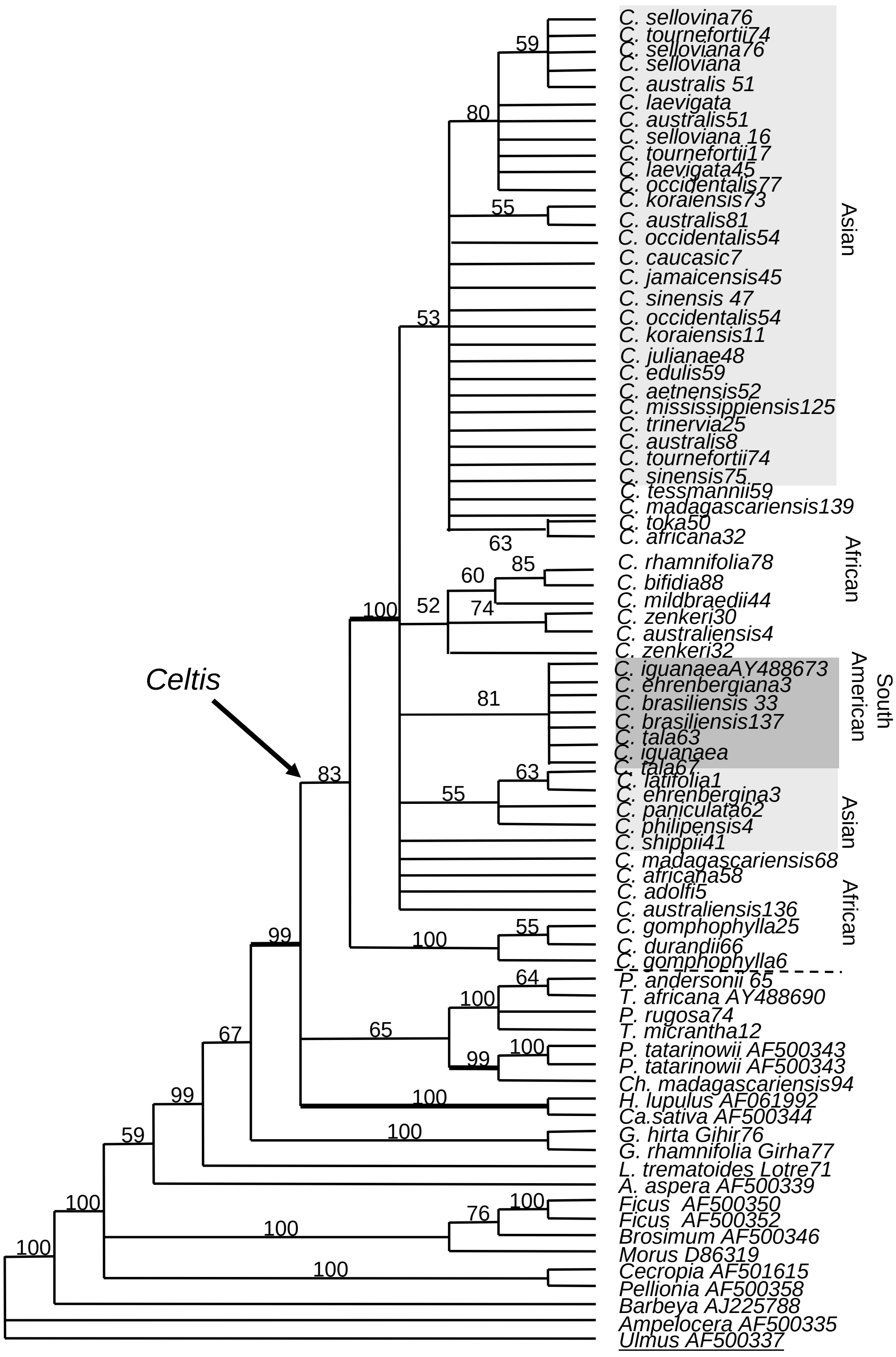


Figure 3.2. Jackknife majority-rule consensus tree (1000 replicates, TBR swapping), support values > 50% are shown, based on *trnL-F* (cpDNA), indels and morphological characters.

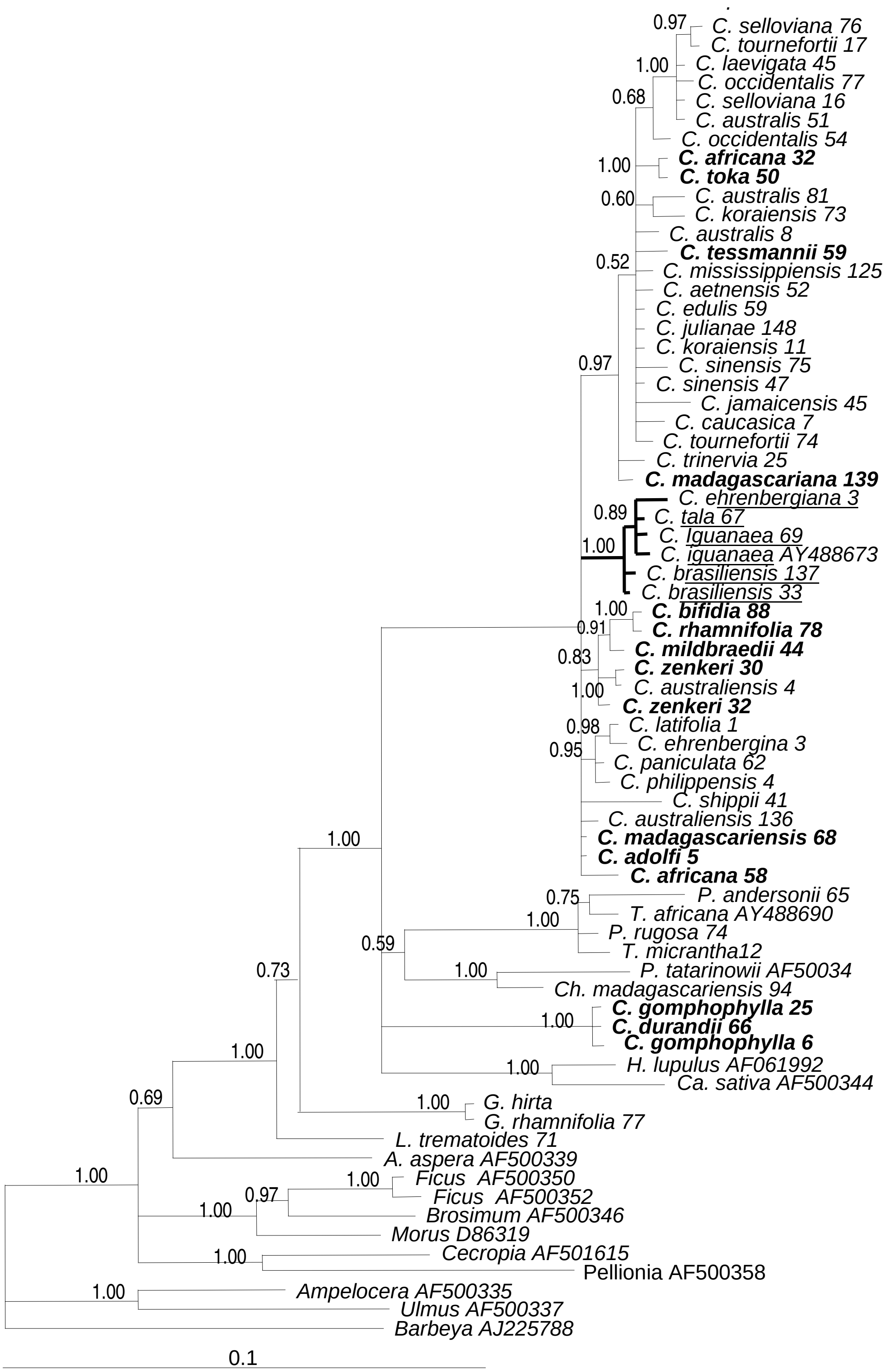


Figure 3.3. Phylogram of the Bayesian majority rule-consensus tree, node label posterior probability values, 50% majority rule consensus tree, (*trnL-F*), 4000000 generations, italic names = Asian, bold = African, underline = South American.

3.6.2 Bayesian analysis

After 4,000,000 generations, the standard deviation of the split frequencies in the simultaneous two MCMC runs in MrBayes was 0.002702, which means that they had converged on the same tree topologies. The proportions of successful exchanges between the chains were 0.40-0.65 (following chain swap information).

Run two had a burn-in of 2000 trees, which means 2.5% of the total 80000 samples. Run 1 also had a burn-in of 4000 trees, (5.2%) of the total 76000 samples, there was no possibility for different burn-in settings for each run, hence 4000 samples were discarded as burn-in before calculating the model parameter values, the trees, and branch lengths.

Bayesian posterior probabilities (p.p.) were overall more or less higher than jackknife support frequencies, but the node leading to the *C. gomphophylla* clade is not identical between the Bayesian and MP topologies (Fig. 3.3) However, the two topologies are congruent (i.e. there are no conflicts), as the *C. gomphophylla* clade is part of a polytomy. The Bayesian topology suggests *Celtis* could perhaps not be monophyletic because of the presence of *Trema*, *Chaetachme*, *Humulus* and *Cannabis* in this polytomy. With the exception of *C. gomphophylla* and *C. durandii*, other *Celtis* formed one clade. There was not any contradiction in comparison with the MP pattern and resolution was better than in the MP search, the South American clade is better resolved (p.p.) and African taxa are more resolved than Asian species but still polytomy appears with this marker (*trnL-F*).

3.7 Discussion

In this chapter we tested our objectives: is African *Celtis* monophyletic within Celtidaceae? Is there a clear relationship between phylogeny and biogeography?

To address these objectives, we studied phylogeny based on *trnL-F* and morphology. Comparing the phylogeny based on this marker, we found some patterns e.g *Celtis gomphophylla* and *Celtis durandii* together are sister to the rest of the others *Celtis* species, especially African and Asian species. There is a large Asian *Celtis* clade which contains 4 African species (see below), and there is another clade for South American species. Most main *Celtis* clades are part of a polytomy, the topology based on *trnL-F* plus morphology has slightly better support values: the support value of the *Celtis* clade is 83% (Fig. 3.1), but in *trnL-F* and indels it is 64%, and patterns are congruent (Fig. 3.1)

The phylogeny based on the *trnL-F* plus coded indel characters was congruent with phylogeny based on *trnL-F* plusindels plus morphology; this means that morphology characters provided better supports, although the *trnL-F* is a relatively fast evolving marker (see chapter 2), it seems that for the phylogeny of *Celtis* we need more markers to get better resolution. The results of the jackknife analysis (maximum parsimony) are not entirely identical but not in conflict with the Bayesian analysis because of the polytomy which can be seen in the *C. gomphophylla* clade. Generally African *Celtis* is more resolved than Asian species e.g. the *C. gomphophylla* clade, *Celtis toka* clade, *Celtis rhamnifolia* clade (informal names), which probably reflects better taxonomic sampling of African species.

In this study we had three objectives: the first one questioned monophyly of African *Celtis* (all of which were included in the analysis): according to this study and Fig. 3.1, 3.2, 3.3 African species are not monophyletic based on t *trnL-F*, and are present within one clade with Asian species. To obtain better patterns we need more markers.

The second objective was about relationships between phylogeny and geographical distribution: we found a clade which contains South American species with value support of 81%. *Celtis toka* and *Celtis africana*, occuring in savannah areas, form here a small clade with value support of 63%.The African species *C. africana*, *C. toka*, *C. malagasica* and *C. tessmannii* are present in a mixed African-Asian clade. There may have been separate dispersal events or taxa are rather similar in this clade. According to our study *C. africana, C. toka* are the same ecological habitat and *C. toka* also occurs in the Yeman in Asia but *C. tessmannii* occurs in rain forest in Africa another species in the mixed clade(Asian and African) is *C. malagasica,* these species occur in different ecological settings, so there may have been separate dispersal events. If we would analyse more Asian species, a firmer conclusion could become possible. All in all, our patterns suggest long-distance dispersal and not vicariance to be a major force in shaping present-day distributions in *Celtis*. Maybe South American species originated by vicariance, as they did not disperse elsewhere, and their morphology does not indicate any difference in seed dispersal capacity.

The third objective was about relationship between phylogeny and morphology. The South American clade (support 81%) fig 3. 2 possessing thorns is classified as a separate subgenus *Mertensia,* and African and Asian taxa are more similar to each other than to South American taxa, presenting a reasonably clear pattern of geographical entities.By adding more taxa from South America it may be to get better resolution for South American Clade.

3.8 Conclusions

Asian and African *Celtis* show patterns that have a few unresolved polytomies. By including morphological characters in the data set, the phylogeny based on *trnL-F*, indel, and morphology is better resolved much higher value support, it means that morphology also provided valuable extra characters. The resolution for the African species is better than for the Asian species, probably because of the taxon sampling. The trees obtained by Parsimony and Bayesian analyses are not identical, but also do not contradict each other, the parsimony-based topology is just further resolved.

Looking at our objectives, the Parsimony Jackknife tree shows that over-all *Celtis* is monophyletic, but for receiving more support for this qualification, we need to use more marker regions than *trnL-F,* such as *matK;* and AFLP™. In the *Celtis* clade, there is also a pattern for South American *Celtis* that can morphologically be distinguished by the presence of thorns. There is no strong clade for African and Asian species of *Celtis,* but a good support for South American species. We need better DNA sequence markers for a better-resolved phylogeny.

Dispersal proves to be the major driving force in distribution pattern of *Celtis,* apart from the South-American taxa, where vicariance may have played a role.

Chapter 4

MACRO-MORPHOLOGY OF AFRICAN *CELTIS* (CELTIDACEAE)

A. SATTARIAN; & L. J. G. VAN DER MAESEN

Summary

Celtis is a genus spread worldwide, and in Africa its species can be seen from North Africa to South Africa, in savannas as well as in rain forests. Three size classes of trees can be seen in *Celtis*: 4-10, 10-25, and 25-45 m tall. The trunks can be cylindrical or sub-cylindrical. In African *Celtis* two types of hairs are distinguished: glandular and non-glandular hairs. The stomata are either paracytic, cyclocytic or anisocytic. Inflorescences in *Celtis* are cymose and fruits are drupes.

4.1 Habit and distribution

Celtis is a widespread genus, which has its natural distribution in Africa, the Mediterranean region, Asia, North and South America, and northern Australia. Outside these areas various species are planted in temperate areas, such as Western Europe, Russia, the Northern USA. In Africa the genus largely occurs from North Africa (*Celtis australis*) to Central and West Africa (*Celtis tessmannii, C. mildbraedii, C. gomphophylla*) as well as in South Africa and Madagascar. The species are seen in savanna regions of both tropical and temperate regions. According to habitat the species range from small-sized tree to large-sized ones (5-45 m), e.g., *C. australiensis* is c. 5 m tall, *C. africana* measures 10-25 m, and *C. tessmannii* is 35-45 m tall. In general three height classes can be seen in *Celtis* (incl. some non-African examples):

Small-sized trees 4-10 m tall: *Celtis australiensis, C. malagasica, C. brasiliensis, C. chichape, C. ehrenbergiana, C. iguanaea,* and *C. loxensis.*
Medium-sized trees 10-25 m tall: *Celtis africana, C. toka,* and *C. orthocanthos.*
Large-sized trees 25-40 m tall: *Celtis tessmannii, C. rigescens, C. paniculata, C. luzonica, C. hildebrandi, C. rubrorenia,* and *C. tetrandra.*

Many species are polymorphic, for instance *C. africana, C. australis,* and *C. toka,* probably due to environmental conditions may be small or medium-sized trees, or their habit can even be expressed as a shrub. In general, Asian and other tropical *Celtis* are medium to large trees and in South America the species are shrubs or small trees.

4.2 Stem, branches and wood

Celtis trunks vary from cylindrical to sub-cylindrical and can be low-branched or branch higher up in the tree. In tropical *Celtis* species normally cylindrical stems are seen e.g. in *C. adolfi-friderici, C. tessmannii, C. tetrandra, C. paniculata, C. luzonica, C. hildebrandi,* and *C. rubrorenia*. A sub-cylindrical stem is present in *C. africana, C. toka,* and *C. australis,* and low-branched stems are present in *C. australiensis, C. malagasica, C. brasiliensis, C. chichape, C. ehrenbergiana, C. iguanaea,* and *C. loxensis.*

According to habitat stems can vary: in the rain forest *C. tessmannii* has a straight cylindrical trunk, while in the savannah *C. africana* has a subcylindrical trunk. In Africa and Asia *Celtis* trunks are cylindrical or sub-cylindrical, while subcylindrical and branched stems are present in South American species.

The bark in African *Celtis* is smooth and whitish to grey; buttresses are present in *C. adolfi-friderici*, *C. toka, C. mildbraedii, C. zenkeri* and *C. wightii*, but not in *C. africana* and *C. australis*.

Celtis yields a lightweight to heavy hard wood with a density of 400-960 kg/m^3 at 15% moisture content (Soerianegara & Lemmens 1993). The hardwood is usually pale brown to pale yellow-brown, occasionally with dark streaks, moderately distinct to indistinct from the wide, white or pale sapwood, grain usually inter-locked, sometimes straight, texture fine to moderately fine, sometimes moderately coarse. Wood of *C. philippensis* and *C. timorensis* has a strong foetid odour when fresh. Growth rings are indistinct or distinct, when distinct they are marked by denser tissue or marginal bands, vessels moderately small to medium-sized, occasionally very small, solitary and in radial multiples of 2-5(-6), occasionally with chalky white deposits, parenchyma moderately abundant, paratracheal vasicentric, aliformately and confluent, the latter irregular, and sometimes apotracheal in marginal or seemingly marginal bands at growth ring boundaries, rays medium-sized, ripple marks absent, occasionally pith flecks present.

Shrinkage is low to moderate and the wood can be seasoned without undue difficulty, with light *Celtis* having a tendency to end-splitting. Tension wood may occur and causes twisting and warping. The wood is moderately soft (light *Celtis*) or hard (hard *Celtis*), moderately strong to strong and fairly tough to tough, although light *Celtis* wood from near the centre of the tree is considerably more brittle. It is moderately easy to work if free of tension wood, though sometimes difficult due to crystalline deposits which blunt tools readily. Planing is difficult and usually gives a rough surface due to the interlocked grain. The wood is very suitable for bent work. It is non-durable and the average service life of *Celtis* test stakes in a graveyard test in the Philippines was 2 years and 4 months. The wood is readily attacked by fungi and insects when exposed to weather or contact with the ground. The hardwood of *C. luzonica* and *C. philippensis*, however, is resistant to dry-wood termites. Staining fungi can cause rapid degrade, even in the log, sapwood is susceptible to *Lyctus* beetles, but in some instance that of *C. luzonica* and *C. philippensis* is reported to be moderately resistant to *Lyctus*. Both sapwood and heartwood are permeable to pressure treatment, retention of 515 kg/m^3 for sapwood and 320 kg/m^3 for heartwood of *C. latifolia* has been determined. The heavier type of *Celtis* wood is used for general construction, wharf and bridge building, decking, industrial flooring, exterior joinery, window-sills, steps, treads, marine piles, wharf fenders, cross arms and railway sleepers. The lighter and more elastic *Celtis* wood is used for light or temporary construction, mouldings, interior finish, furniture and cabinet work, tool handles, tennis rackets, horizontal bars, posts, boxes, plywood and veneer. The wood is also suitable for the production of pulp for paper. Wood of *Celtis africana* is white to yellowish and medium hardness. It is tough and strong, and polishes well. It is a good timber suitable for making planks, shelving, yokes, tent-bows and furniture. The African people have used it to make a variety of household articles and it is also thought to have magical properties. The wood is mixed with crocodile fat as a charm against lightning; many people believe that it has the power over evil and that pegs of wood driven into the ground will keep witches away.

4.3 Leaves and indumentum

Celtis leaves vary from elliptic to ovate and lanceolate, ovate-lanceolate is seen in *Celtis australis, C. africana, and C. zenkeri,* elliptic to lanceolate are found in *Celtis gomphophylla* and *C. bifida*. The leaf base is rounded and normally unequal-side at base. The apex is rounded in *Celtis malagasica* and acuminate in *Celtis bifida, C. zenkeri.* Leaf size varies from small size in *Celtis* *africana, C. bifida* (4-8 cm long & 3-6 cm wide) to big one (9-16 cm long & 6-12 cm wide) which are seen *Celtis gomphophylla, C. zenkeri, and C. prantlii* (Fig. 4.15-16).

In African *Celtis* different types of hairs can be distinguished: glandular and non-glandular ones, with various densities of hairs on lower and upper side of the leaf, but on the whole in African *Celtis* two types of hairs are discerned, glandular and non-glandular hairs (Fig. 4.1-4). 10 samples from different localities have been measured, see table 4.1.

Table 4.1 Description of indumentum in African *Celtis*. D: density in % of leaf surfaces.

Species	**D/upper %**	**D/lower %**	**Hair types**
Celtis adolfi-friderici	10	70	1. Glandular hairs, unicellular and small with a little globular apex 2. Non-glandular hairs often thick-walled, unicellular with an acute apex
C. africana	50	70	Non-glandular hairs often thick-walled and with acute apex
C. australis	40	80	Non-glandular hairs often thick-walled and with acute apex
C. bifida	40	60	Non-glandular hairs often thick-walled and with acute apex
C. gomphophylla	30	40	Non-glandular hairs, small with acute apex
C. mildbraedii	_____	_____	Non-glandular hairs, acute apex, hairs only seen on venation
C. prantlii	_____	_____	Non-glandular hairs, acute apex, hairs only seen on venation
C. toka	30	60	1. Non-glandular hairs 2. Non-glandular but multicellular and branched
C. tessmannii	10	30	1. Non-glandular hairs 2. Non-glandular but multicellular and branched
C. wightii	_____	_____	Non-glandular hairs, acute apex, hairs only seen on venation
C. zenkeri	10	70	Non-glandular hairs, unicellular, surface scabrous

4.4 Stomatal patterns

In African *Celtis* the pattern of stomata in epidermis is useful and valuable as an additional taxonomic character. It is often easy to recognize and it enables us to distinguish species in combination with the other leaf characters. Stomates are usually classified by relationships of their subsidiary cells (epidermal cells associated with the stomata and morphologically distinguishable from the surrounding epidermal cells) to one another and to the guard cells.

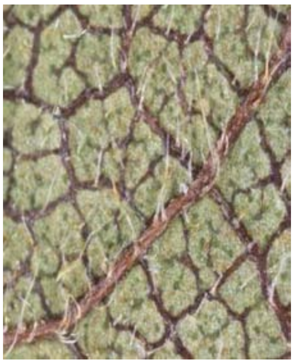
Small fragments of the leaflets of herbarium specimens were dehydrated in boiling water. Manually prepared samples were made from the lower leaf surface; samples were then bleached in diluted household bleach. All samples were observed by light microscopy under a magnification of 40 times and all specimens were photographed. The terminology of Wilkinson (1979) is used to describe the stomata.

A paracytic pattern (stomata surrounded by two subsidiary cells parallel to the guard cells) is found in *Celtis africana, C. tessmannii, C. mildbraedii, C. zenkeri, C. prantlii,* and *C. bifida* (Fig. 4.5-6). Anisocytic stomata (stomata surrounded by three subsidiary cells, of which one is distinctly smaller) are seen in *Celtis adolfi-friderici*, and *C. toka* (Fig. 4.7-8), while cyclocytic stomata (stomata surrounded by subsidiary cells form one or two narrow rings around the guard cells, the number of cells in each ring usually being four or more) are found in *Celtis gomphophylla*, and *C. africana* (Fig. 4.9-10). In all, three patterns are discernible, but no correlation is seen with the locality or habitat.

Indumentum

Stomata, fruits

Infloresc., leaves



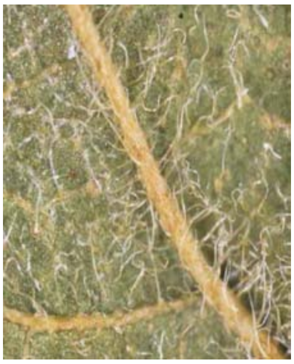
4.1 *Celtis africana*

Paracytic stomata

4.5 *Celtis tessmannii*

4.6 *Celtis zenkeri*

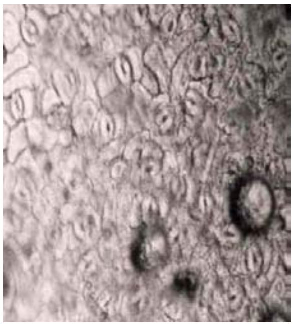
4.13 *Celtis australis*



4.2 *Celtis australis*

Anisocytic stomata

4.7 *Celtis toka*



4.8 *C. adolfi-friderici*

4.14 *Celtis laevigata*

4.3 *Celtis tessmannii*

Cyclocytic stomata

4.9 *Celtis africana*

4.10 *C. gomphophylla*

4.15 *Celtis prantlii*

4.4 *Celtis prantlii*

4.11 *Celtis mildbraedii*

4.12 *Celtis australis*

4.16 *Celtis tessmannii*

Figure 4.1 – 4.16. Different types of indumentum: 4.1 – 4.4; stomata: 4.5 – 4.10; fruits: 4.11 & 4.12; inflorescences: 4.13 & 4.14; leaves: 4.15 – 4.16.

4.5 Inflorescences and flowers

Inflorescences in *Celtis* are cymose or fasciculate, the lower ones usually bear many predominantly ♂ flowers, the upper ones have a few longer-pedicelled hermaphrodite flowers. The flowers have 4-5(6) sepals, free or almost imbricate stamens as many as sepals, anthers are ovate 3-5 mm long Female flowers have a sessile ovary, 1-locular; style 1 or 2-branched (Fig. 4.13-15), pollination of the *Celtis* is by wind and insects but wind-pollination is very common, For further details see the descriptions of the species.

4.6 Fruits

Generally *Celtis* have drupe-type fruits, with size variation and colour as well; the smallest *Celtis* fruits measure 4 to 8 mm in diameter, the largest ones are 12 to 20 mm. In *Celtis mildbraedii* the fruit is four-sided, and most other African *Celtis* are rounded to lanceolate in shape. The fruit colour starts green, turns to orange or yellow and then becomes black (Fig. 4.11-12). The embryo is protected by the hard, persistent and durable endocarp. The endocarp is variously sculptured (ridged); for more details see Chapter 6 in this thesis.

Chapter 5

POLLEN MORPHOLOGY OF AFRICAN *CELTIS* (CELTIDACEAE)

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Summary

Pollen morphology of all African *Celtis* species was examined and compared with that of some Asian species, using light and scanning electron microscopy. The pollen grains are triporate and more or less spheroidal. Two pollen types could be distinguished based on a feature of the apertures and the density of the surface ornamentation.

5.1 Introduction

Celtidaceae (formerly Ulmaceae-Celtidoideae) (Elias 1970, Grudinskaya 1967, Judd et al. 1994, Terabayashi 1991, Ueda et al. 1997) comprise ca. 150 species classified in 9 genera, distributed in the Northern Hemisphere and in Africa, up to southern Africa. Some species of the family are ornamental, or used for timber and reforestation. In Celtidaceae and Ulmaceae two types of pollen have been shown, the *Celtis*-type and the *Ulmus*-type. An exception is *Zelkova* that, although belonging to the Celtidaceae has pollen grains of the *Ulmus*-type (Erdtman 1943, 1972).

Based on exine sculpturing and structure, pollen grains of the Ulmaceae can be placed into six different types (Takahashi 1989). Members of the Ulmaceae all share tetra-or pentaporate, oblate to spheroidal pollen grains varying in size from 23 µm to 42 µm.

Within the Celtidaceae five types of pollen grains have been described (Takahashi 1989):

1) *Ampelocera* pollen is distinguished by being periporate or tetra- to pentaporate and having pallisade rather than granular ectexine.

2) *Chaetachme* grains are similar to those of *Ampelocera* but have a very thin endexine and a perforated exine with spinules.

3) A densely warty exine and a middle granular layer distinguish the triporate pollen grains of *Gironniera*.

4) Densely spaced warts and microechinules and the absence of a granular layer in the exine characterize *Lozanella*, *Parasponia*, and *Trema*. Their grains are radially or bilaterally symmetrical and either diporate or triporate.

5) *Aphananthe*, *Celtis*, and *Pteroceltis* are tri- to pentaporate and all have a middle granular layer in the exine.

Data on pollen morphology of *Celtis* are lacking especially for the African species. The aim of the present research was to study the diversity and range of variation of the pollen-morphological characters in African *Celtis* spp. and to check the utility of these data to improve the taxonomy of the African species.

Table 5.1. Pollen material studied.

Taxon	**Collection**	**Herb.**	**Living**	**Place of collection**
C. africana Burm.f.	E. Westphal et al. 2326	WAG		Ethiopia
C. adolfi-friderici Engl.	Mildbraed 825	K		Cameroon
C. bifida Leroy	S.O. Connor 44	MO		Madagascar
C. gomphophylla Baker	J.D. & E.G. Chapman 9361	L		Malawi
C. mildbraedii Engl.	A.J.M. Leeuwenberg 4078	WAG		Ivory Coast
C. philippensis Blanco	F.A.W. Schram 12364	WAG		Malaysia
C. prantlii Priemer ex Engl.	M. Le Testu 1479	WAG		Gabon
C. tessmannii Rendle	J.J. Wieringa 4665	WAG		Gabon
C. toka Engl.	W.J.J.O. de Wilde 5287	WAG		Angola
C. zenkeri Engl.	R. Letouzey 12155	WAG		Cameroon
C. australis L.	H.H. de Leeuw 487	WAG	√	Wageningen Bot. Gard.
C. occidentalis L.	H.H. de Leeuw 493	WAG	√	Wageningen Bot. Gard.
C. sinensis Pers.	H.H. de Leeuw 483	WAG	√	Wageningen Bot. Gard.
C. tournefortii Lam.	H.H. de Leeuw 486	WAG	√	Wageningen Bot. Gard.

5.2 Materials and methods

The herbarium material was taken from the following herbaria: WAG, K, MO and L. All extant African species have been studied, and some Asian species were included for comparison. The living material was obtained from the Wageningen Botanical Gardens (Table 5.1).

Fertile anthers were processed according to the standard acetolysis method (Erdtman 1943). For scanning electron microscopy (SEM) observation, pollen grains from mature anthers were mounted using a fine needle on aluminum stubs with double-sticky tape. Prepared stubs were sputter-coated with gold in 2-6 minutes (Balzersunion, Sputter-Anlage 07120). After coating, the specimens were observed with a Jeol JSM 5200 scanning Electron Microscope, at 15-25 KV. Measurements of pollen grains were taken from the SEM micrographs. The averages of polar and equatorial axes were based on measurements of 10-15 pollen grains.

All SEM photomicrographs were taken at the laboratory of Plant Cell Biology, Wageningen University, the Netherlands. The pollen morphological terminology follows that by Punt et al. (1999) and Nilsson & Le Thomas (1999).

5.3 Results

Pollen grains of African *Celtis* are small to medium sized, triporate, and more or less spheroidal. Surface ornamentation is verrucate with a varying density of structural elements. All measurements are given in Table 5.2.

Size

The size of the pollen grains ranges from 17 µm (*C. tessmannii*: P=17.27µm, E=18.4 µm) to 37 µm (*C. occidentalis*: P=32.5, E=37.5). According to Erdtman (1943) the pollen of *Celtis* can be classified into the category small to medium size. The African species generally have smaller pollen grains than the Asian species.

Table 5.2. Pollen morphological data of *Celtis* species. Polar axis (P), equatorial diameter (E), ratio P/E, shape, thickness of exine (L), aperture dimensions (A), density of sculptural elements (S). All measurements in µm, density of sculptural elements: number per 100 µm^2.

Taxon	**Distribution**	**P**	**E**	**P/E**	**Shape**	**L**	**A**	**S**
C. africana	Africa	(25-) 25.4 (-27.5)	(22.5-) 25.3 (- 27.5)	0.98	spheroidal	2.5	2.8*1.4	170
C. adolfi-friderici	Africa	(17.5-) 17.5 (- 20)	(17.5-) 18.25 (- 20)	0.95	spheroidal	1.25	1.3*2	425
C. australis	Asia	(27.5-) 30 (- 35.5)	(30-) 32.5 (- 32.5)	0.92	spheroidal	2.5	6.1*6.5	250
C. bifida	Africa	(20-) 22.75 (- 25)	(20-) 22.5 (- 25)	1.01	spheroidal	1.25	4.5*4.5	162
C. gomphophylla	Africa	(22.5-) 25 (- 27.5)	(22.5-) 24.5 (- 25)	1.03	spheroidal	1.25	3*1.5	150
C. mildbraedii	Africa	(17.5-) 21.07 (-22.5)	(20-) 22.17 (- 22.5)	0.94	spheroidal	2.5	8*3	
C. occidentalis	Asia	(30-) 32.5 (- 40)	(37.5-) 37.5 (- 42.5)	0.87	Oblate	1.25	_	_
C. philippensis	Asia	(17.5-) 19.37 (- 22.5)	(20-) 22.17 (-22.5)	0.88	Oblate	2.5	7.2*6	277
C. prantlii	Africa	(17.5-) 20.07 (- 22.5)	(17.5-) 20.5 (- 22.5)	0.97	spheroidal	2.5	7*8	_
C. sinensis	Asia	(22.5-) 24.3 (- 30)	(27.5-) 30.67 (- 35)	0.79	Oblate	3	_	600
C. tessmannii	Africa	(15-) 17.27 (- 20)	(15-) 18.4 (- 20)	0.93	spheroidal	1.25	4*5	600
C. toka	Africa	(20-) 21.12 (- 22.5)	(22.5-) 22.95 (- 25)	0.92	spheroidal	1.25	10*9	340
C. tournefortii	Asia	(17.5-) 25.6 (- 22.5)	(25-) 29 (- 37.5)	0.88	Oblate	3	_	_
C. zenkeri	Africa	(20-) 22.64 (-27.5)	(17.5-) 19.5 (- 22.5)	1.16	Prolate	2.12	15*8	340

Shape

The ratio between the mean polar axis (P) and the mean equatorial diameter (E) is used to assign the pollen grains to shape classes. According to this ratio the shape of the majority of *Celtis species* is spheroidal and a minority is slightly oblate or prolate (using the following delimitations: P/E 0.75-0.9: oblate, 0.9-1.1: spheroidal, 1.1-1.25: prolate spheroidal). All African species show spheroidal pollen, Asian *Celtis* species tend to be more oblate (Fig. 5.2).

Apertures

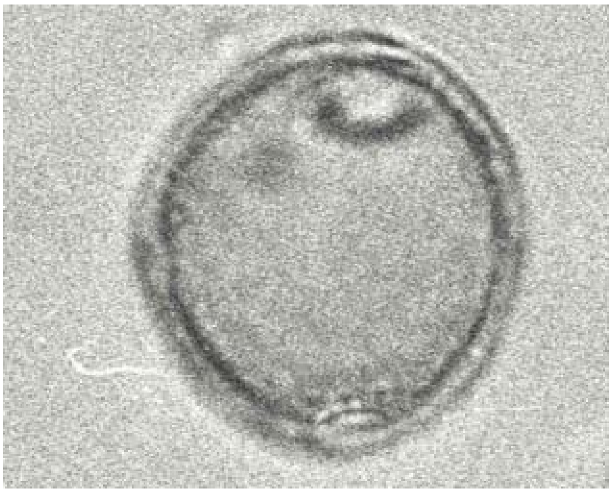
Pollen grains of African *Celtis* are triporate. The pores are round to oval. The majority of the pollen shows a sunken area surrounding the pore. This circular sunken area has only been observed in SEM, not in LM and this could be due to desiccation. However, in certain species this feature is never observed, while, on the other hand, it was observed in fresh, non-acetolysed material of *Celtis australis*, indicating that it is a feature characteristic of a group of species.

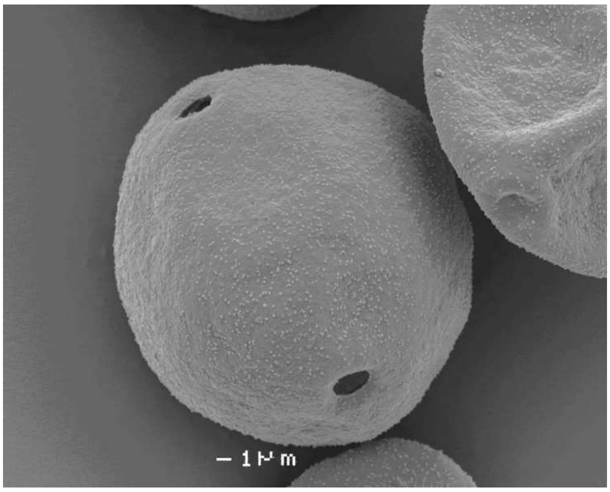
Surface ornamentation

Surface sculpture is more or less roughly verrucate, with irregularly shaped elements which differ in size. The density of the elements ranges from 150-450 / 100µm^2 (10x10 µm area on SEM photos).

Figure 5.1. Pollen grains of some African *Celtis* species (left: light microscopy, right: electron microscopy).

Celtis africana pollen type:

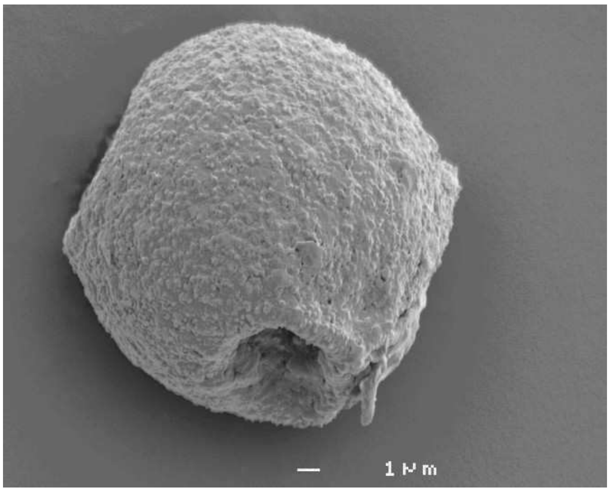

Celtis africana



Celtis africana

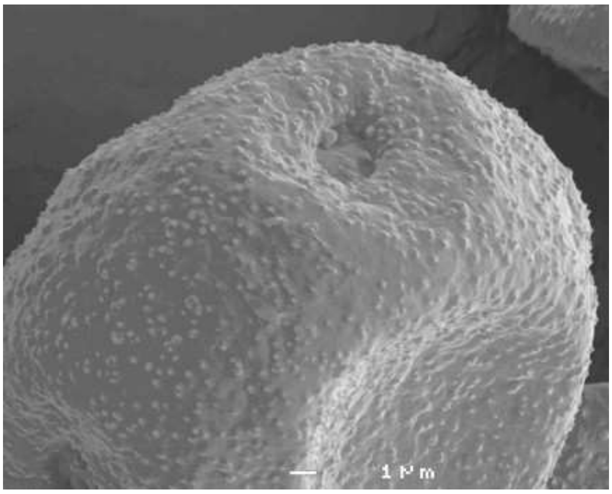
Celtis australis pollen type:


Celtis australis



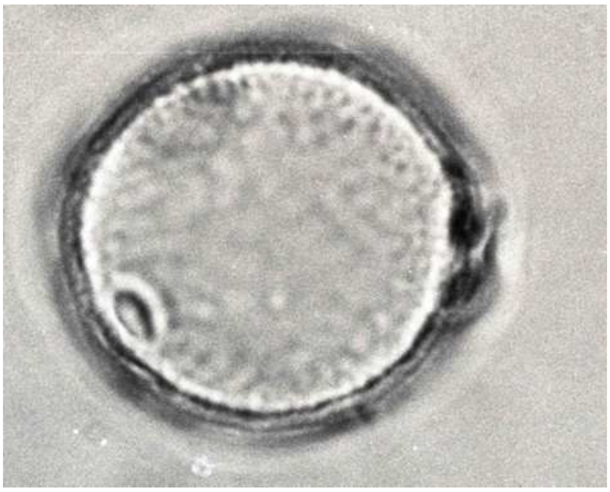
Celtis australis


Celtis bifida

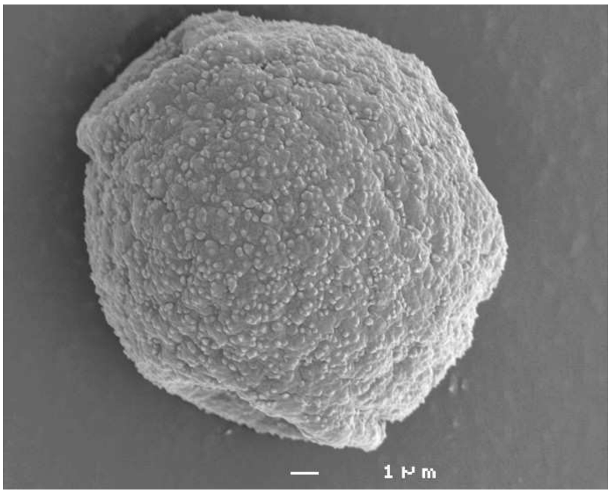


Celtis bifida

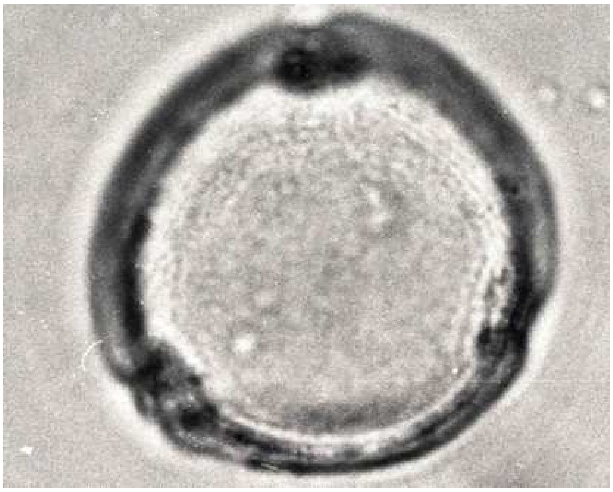
Figure 5.1. Continued.



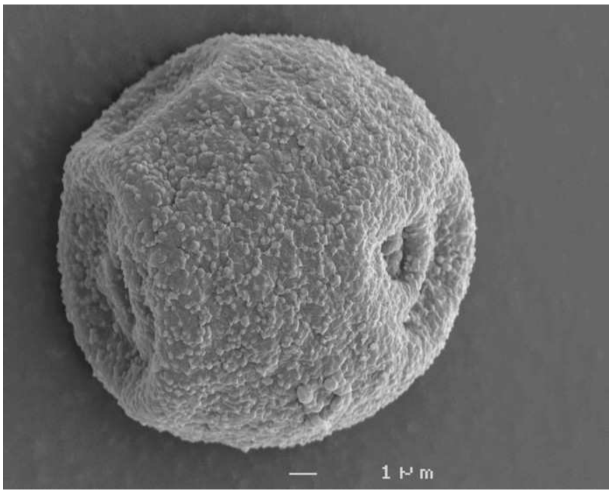
Celtis philippensis



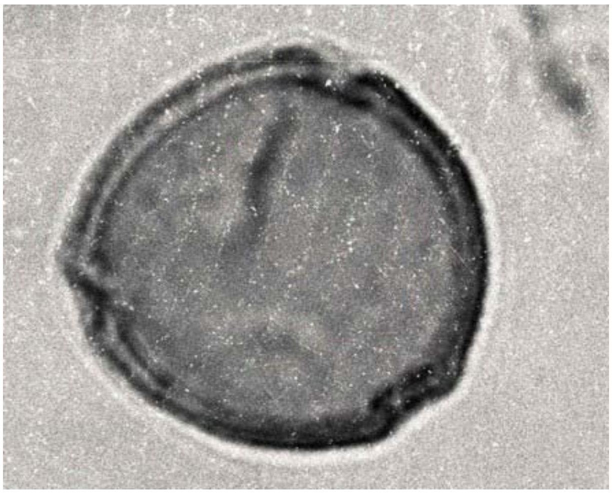
Celtis philippensis



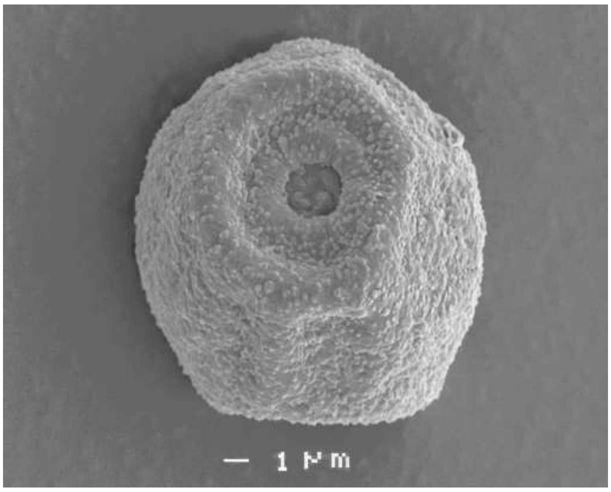
Celtis prantlii



Celtis prantlii



Celtis toka



Celtis toka

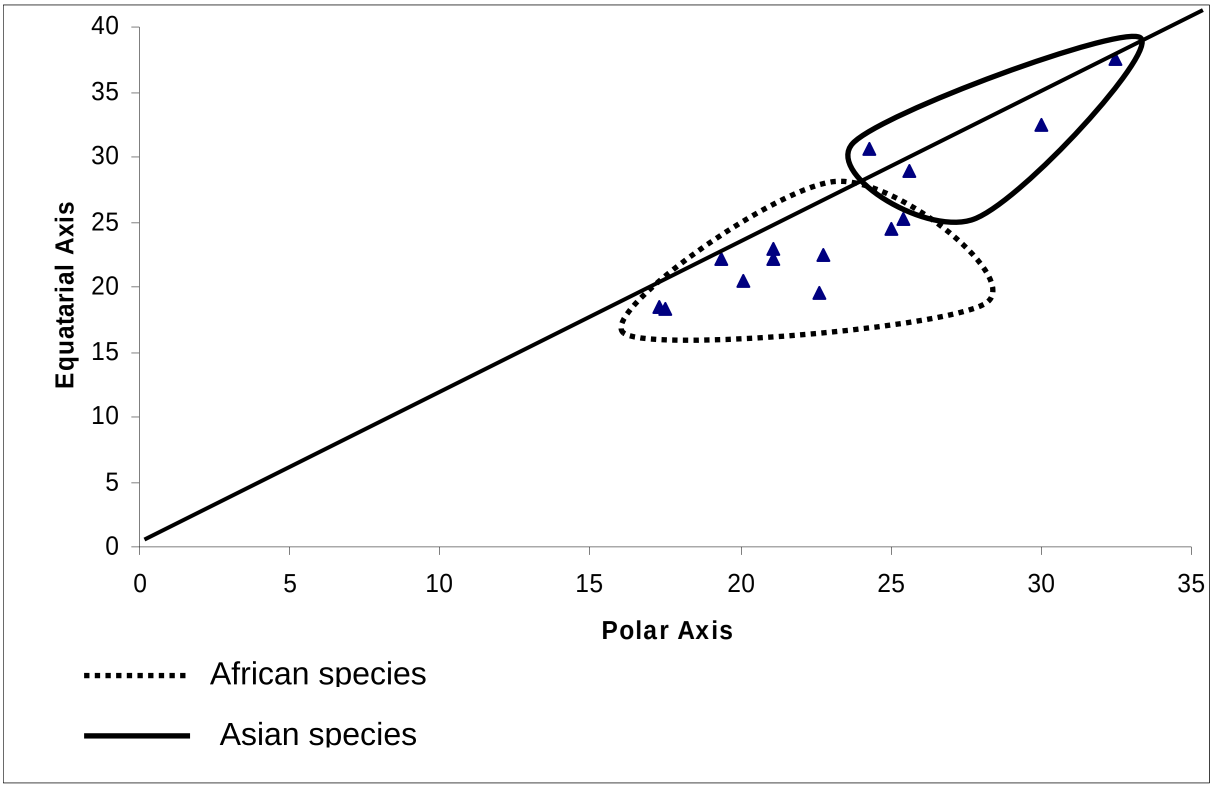


Figure. 5.2. Means of E/P axes (Asian and African *Celtis*).

Description of *Celtis* pollen types

Based on the absence/presence of the sunken area around the pores and the surface ornamentation, two pollen types can be described for *Celtis*:

C. australis type: Polar axis 17.5-30 µm, equatorial diameter 18-32 µm, sunken area around aperture present, sculptural elements irregularly arranged, density of sculptural elements 162-600 /100µm². This type is present in *C. adolfi-friderici, C. australis, C. bifida, C. mildbraedii, C. philippensis, C. prantlii, C. tessmannii, C. toka,* and *C. zenkeri* (Fig. 5.1).

C. africana type: Polar axis 22.5-27.5 µm, equatorial diameter 22.5-27.5 µm, sunken area around aperture absent, sculptural elements regularly arranged, density of sculptural elements 150-170 µm/100µm². This type is present in *C. africana* and *C. gomphophylla* (Fig. 5.1).

5.4. Discussion and conclusion

In general *Celtis* pollen is not very variable. It is triporate, spheroidal and small- to medium-sized. Most of the species show a sunken area around the pore in SEM (not in LM). This area is never present in pollen grains of *C. africana* and *C. gomphophylla*.

According to the P/E ratio and size a distinction can be made between Asian and African *Celtis* species (Fig. 5.2): pollen grains of Asian *Celtis* species *(Celtis occidentalis, C. sinensis, C. tournefortii)* are bigger and more oblate than those of African species. Furthermore, among African species the tropical species (*C. tessmannii, C. adolfi-friderici*) have smaller pollen than the species from drier areas (*C. africana, C. gomphophylla)*.The differences in pollen morphology of African *Celtis* species do not seem to be correlated with other taxonomic characters.

Chapter 6

ENDOCARP MORPHOLOGY OF AFRICAN *CELTIS* (CELTIDACEAE)

A. SATTARIAN & L. J. G. VAN DER MAESEN

Published in Blumea 51: 2 (2006)

Summary

Endocarp morphology of 14 species of mainly African *Celtis* was examined using light and scanning electron microscopes. Macro- and micro-morphological characters included endocarp shape, colour, size, surrounding rim and SEM examination of the outer layer of the endocarp. Different classes of shape and sculpture were recognised. A key for the identification of the investigated taxa based on endocarp characters is provided.

Key words

Celtis, Africa, endocarp, sculpture, shape.

6.1 Introduction

Celtidaceae (formerly Ulmaceae-Celtidoideae) (Elias 1970; Grudzinskaya 1976; Judd et al. 1994; Omori et al. 1993, Omori & Terabayashi 1991, Ueda et al. 1997) comprise ca. 150 species classified in 9 genera, distributed in the Northern Hemisphere and in Africa, up to southern Africa. Some species of the family are ornamental; some are used for timber and reforestation.

In the flora of Africa, Celtidaceae is a small family with the main genus *Celtis*, at present represented by 12 species. The habitat of *Celtis* species reaches from North Africa (Algeria, Libya and Morocco) to South Africa and Madagascar. Several tree species are found in the rain forest (*Celtis tessmannii* Rendle*, C. adolfi-friderici* Engl.) or in semi-deciduous forest (*C. prantlii* Engl., *C. zenkeri* Engl.). Other *Celtis* are shrubs or small trees of rain forest undergrowth (*C. gomphophylla* Baker*)*, of the forest/savannah boundary, or sometimes of montane forest (*C. africana* Burm.f.). One species (*C. toka* Forssk.) is a fairly large tree with a compact crown, living beside streams or planted in villages in the Sudano-Sahelian zone.

The fruits in the Ulmaceae and Celtidaceae families are of two general types: dry and variously winged samaras or fleshy drupes, respectively. A wide variety of dry winged fruits occurs in the Ulmaceae and, along with endocarp features, are useful in distinguishing genera. Endocarps in the Ulmaceae are generally thin and soft except for *Zelkova* and *Hemiptelea*. Drupes characterize all genera of the Celtidaceae except for *Pteroceltis*, which has a winged drupe. Size ranges from approximately 1-2 mm in diameter in *Lozanella*, *Parasponia*, and *Trema* to up to 23 mm broad in *Ampelocera glabra*. Endocarps in the Celtidaceae are usually globose (except for *Ampelocera*, which can be ellipsoid, and *Gironniera* and *Lozanella*, which are lenticular), thick-walled and hard due to calcium carbonate in *Celtis* and sclereids in *Aphananthe* (Manchester 1989). Reticulate surface sculpturing is found in *Celtis*, *Peteroceltis*, *Trema*, and *Parasponia. Pteroceltis* has spherical endocarps very similar to *Celtis* except for a pair of prominent rounded wings.

Table 6.1. List of specimens used in (B/SEM) endocarp studies. B = binocular, SEM = electron microscope.

Taxon	**Collection**	**Herb.**	**Country of origin**
C. adolfi-friderici Engl.	Mildbraed 825	K	Cameroon
C. africana Burm.f.	Dahlstrand 579	C	South Africa
C. australiensis Sattarian	Chesterfield, E.A. 389	L, PERTH	Australia
C. australis L.	Sattarian 03BG15801	WAG	Italy (WAG Bot. Gard.)
C. bifida Leroy	O'Connor 44	K	Madagascar
C. gomphophylla Baker	Chapman 9361	MO	Malawi
C. malagasica Sattarian	Phillip, P.B. 2938	MO	Madagascar
C. mildbraedii Engl.	Leeuwenberg 4078	WAG	Ivory Coast
C. philippensis Blanco	Soepadmo 7225	L	Malaysia
C. prantlii Priemer ex Engl.	Le Testu 1479	WAG, P	Gabon
C. tessmannii Rendle	Liben 2254	BM	D.R. Congo
C. toka Forssk.	De Wilde, W.J.J.O. 5287	WAG	Cameroon
C. wightii Planch.	Ludanga 782	C	Tanzania
C. zenkeri Engl.	Leeuwenberg 6227	WAG	Cameroon

The cotyledons are usually folded in the Celtidaceae. *Celtis* is distinguished by its broad contorted cotyledons (Killip & Morton 1931). Seed coat (testa) features vary among the genera. *Celtis*, *Chaetachme*, and *Pteroceltis* have the most elaborate seed surface sculpturing in the family with many holes. *Lozanella*, *Parasponia*, and *Trem*a have a lineate seed coat surface (Takaso & Tobe 1990).

The drupaceous fruits of the Celtidaceae vary in colour from bright yellow to orange, deep red, and purple and are primarily bird-dispersed. *Celtis philippensis* var. *wightii* which grows in coastal forests in Melanesia has been suggested to be water-dispersed (Soepadmo 1977).

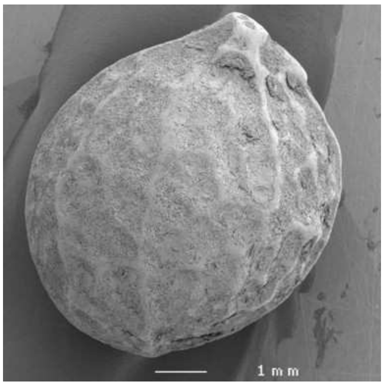
Most systematists agree that data concerning the macro- and microstructure of fruits and seeds are very significant for the classification of Angiosperm taxa. Heywood (1971) drew attention to the importance and impact of scanning electron microscopic imaging in the study of systematic problems, as very valuable information has been provided by this technique. During the last decades, scholars have applied scanning electron microscopy (SEM) to morphological studies of seeds and small fruits. Micro morphology and ultra-structural data have contributed useful information for evolution and classification of seed and fruit plants and play an important role in the modern synthetic systems of Angiosperms.

Most of the following studies focused on intrageneric seed coat variation in various structures (see Aniszewski et al. 2001); for the colours of seeds refer to Dahlgren & Clifford (1982).

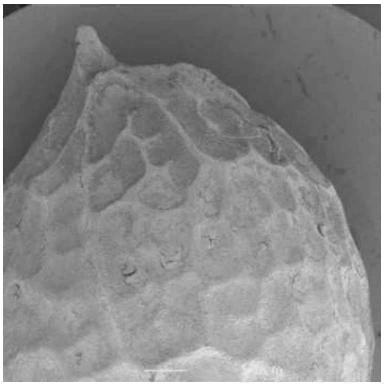
In Celtidaceae, external seed morphology and germination were studied by Canne 1980; Barthlott 1981; Whiffin 1972; Polhill 1964; Metcalfe & Chalk 1950; and Corner 1976. These studies were focused on germination, extraction, nursery practice, germinative energy, and germinative capacity, while investigations on seed and not so much on endocarp morphology, and sculpture of endocarp are lacking. The present study set out to fill some of the gaps in our knowledge, focusing on the micro- and macro-morphological (binocular and SEM) characters of endocarp of (mainly) African *Celtis* spp. to decide on the importance of endocarp characters as a criterion for separating species within this genus.

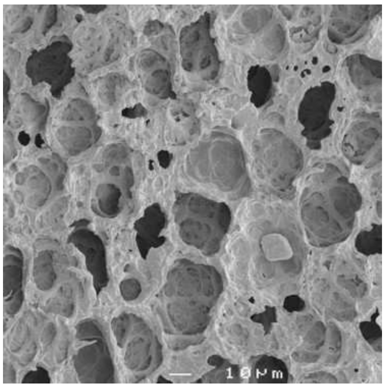
Fig. 6.1. SEM micrographs of *Celtis* species:


Celtis adolfi-friderici



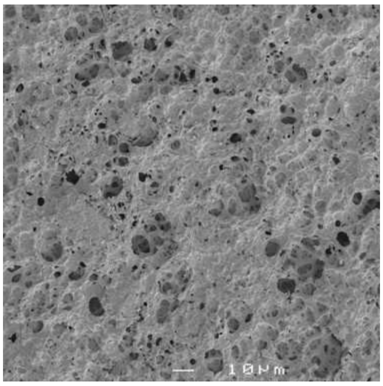
Celtis australis


Celtis tessmannii

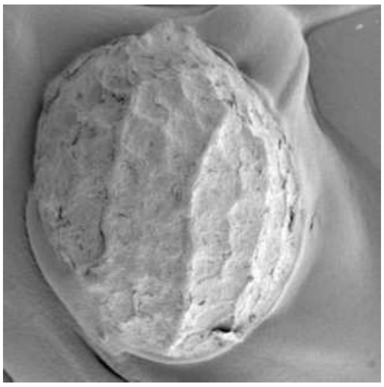


Celtis adolfi-friderici

Celtis australis

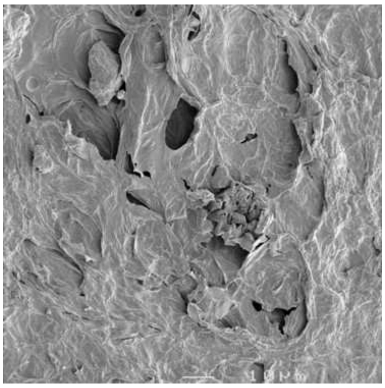


Celtis tessmannii

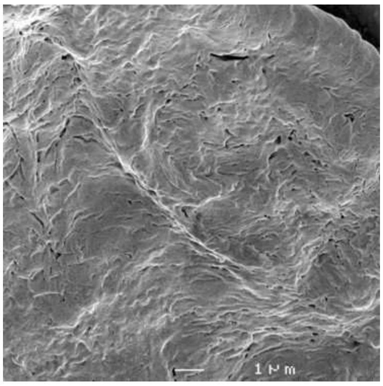

Celtis africana

Celtis mildbraedii

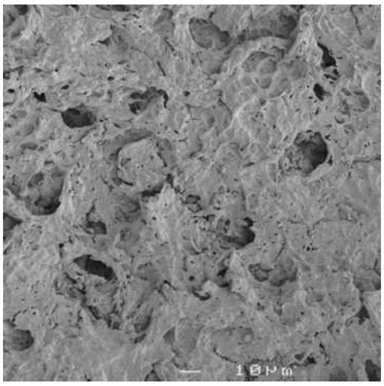

Celtis wightii



Celtis africana



Celtis mildbraedii



Celtis wightii

Table 6.2. Endocarp morphology of African *Celtis* spp., *C. philippensis s.s.* and *C. australiensis.*

Taxon	**Size (mm)**	**Colour**	**Shape**	**Texture**
C. adolfi-friderici	10 x 9 x 8	white	Globose to ellipsoid, acuminate, reticulate	rough
C. africana	4 x 3 x 2	grey	Lenticular-ovoid, reticulate	rough
C. australiensis	6 x 4 x 4	white	Ovoid-acuminate	smooth
C. australis	6 x 6 x 5	greyish white	Ovoid, acuminate reticulate	rough
C. bifida	6 x 5 x 4	white	Ovoid, acuminate reticulate	rough
C. gomphophylla	4 x 3 x 2.5	dark brown	Angular-ovoid	rough
C. malagasica	10 x 8 x 9	cream	Globose to elliptic	smooth
C. mildbraedii	6 x 5 x 3	grey	Rhomboid, reticulate	rough
C. philippensis s.s.	6 x 5 x 5	grey	Ovoid	smooth
C. prantlii	8 x 6 x 5	white	Ovoid, acuminate, reticulate	smooth
C. tessmannii	11 x 10 x 8	brown	Lenticular	rough
C. toka	7 x 6 x 6	grey	Ovoid-acuminate	smooth
C. wightii	8 x 6 x 5	white	Ovoid-acuminate	smooth
C. zenkeri	5 x 4 x 4	cream	Ovoid-acuminate, reticulate	rough

6.2 Materials and methods

Most of the endocarp material was taken from herbarium vouchers, especially from the herbarium at Wageningen (WAG), but also from sheets on loan from other herbaria (B, BM, BR, C, K, L, MO, P, PERTH, W), see also Table 6.1.

In general endocarps of *Celtis* can be inspected easily. Mature fruits were taken from the specimens, as far as available. The dried fruits were boiled in water for 10 min. and brushed clean, then rinsed in water with bleach for 10 min. to obtain clean endocarps. These were first examined by binocular (B) or light microscope (LM). Subsequently endocarps were mounted on stubs with double adhesive tape. The stubs were sputter-coated with gold-paladium for 2-3 min. in a Polaron Equipment Ltd. SEM coating unit E5100. After coating, the specimens were examined with a Joel 5200 scanning electron microscope. All photomicrographs were taken at the Department of Plant Cytology and Morphology, SEM laboratory, Wageningen University, the Netherlands.

Table 6.2. Continued.

Ratio diam/length	Ridges	Sculpture outline	Outer layer
9/10	A few prominent longitudinal ridges	Polygonal, not Isodiametric	Raised boundaries at different directions
3/4	One prominent ridge	Polygonal, not Isodiametric	Boundaries curvy, not raised much; tip beaked
4/6	Two ridges	Polygonal, not Isodiametric	Boundaries curvy, not raised
6/6	Two prominent longitudinal ridges	Polygonal, not Isodiametric	Raised boundaries at different directions
5/6	Two prominent ridges	Polygonal, not Isodiametric	Raised boundaries at different sides
3/4	One ridge, muricate surface	Not polygonal, not Isodiametric	Few boundaries from the bottom to middle, one side is flat, apex beaked
8/10	Two prominent longitudinal ridges	Polygonal, not Isodiametric	Boundaries curvy, semi raised
5/6	One ridge	Polygonal, not Isodiametric	Boundaries curvy and raised
5/5	One ridge	Not polygonal, Isodiametric	Boundaries faint, smooth
6/8	One ridge	Polygonal, not Isodiametric	Boundaries differ, but not raised so much
10/11	A few ridges	Polygonal, Isodiametric	Boundaries, curvy, raised
6/7	One ridge	Polygonal, Isodiametric	Boundaries curvy
6/8	One ridge	Polygonal, not Isodiametric	Boundaries faint
4/5	One ridge and transverse connecting ridges	Polygonal, not Isodiametric	Boundaries curvy, not raised much

6.3 Results

Endocarp shape

The shape of the endocarp showed variation among the African *Celtis*. Most endocarps vary from ovoid-acuminate to ovoid. They are ovoid-acuminate in *Celtis australis*, *C. bifida*, *C. philippensis*, *C. prantlii*, *C. toka*, *C. wightii*, and *C. zenkeri* (Table 6.2), lenticular-ovoid in *C. africana* and *C. tessmannii*, angular-ovoid in *C. gomphophylla*, and globose to ellipsoid in *C. adolfi-friderici*.

Two classes of endocarp epidermis surface can be distinguished: smooth and rough. *Celtis philippensis* has a smooth epidermis, and *C. adolfi-friderici*, *C. africana*, *C. gomphophylla*, *C. mildbraedii*, *C. tessmannii*, *C. zenkeri*, and *C. bifida* have a rough epidermis.

Endocarp size

The size of the endocarps also varies. The range is from the smallest one (4 x 3 x 2 mm) in *Celtis gomphophylla* and *C. africana* to the largest one (11 x 10 x 8 mm) in *Celtis tessmannii*, but the majority of the endocarps measure about 6 x 5 x 5 mm in *Celtis philippensis*, *C. toka*, *C. wightii*, *C. zenkeri*, *C. mildbraedii*, *C. australis*, and *C. bifida*. The endocarp size is a good character, useful to separate *Celtis adolfi-friderici*, *C. tessmannii* from the rest of African *Celtis*.

KEY TO AFRICAN AND SOME OTHER *CELTIS* SPP.
BASED ON ENDOCARP CHARACTERS

1 a Endocarp angular-ovoid, dark brown .... ***C. gomphophylla***
b Endocarp ovoid-acuminate, lenticular, or globose, other colours 2
2 a Endocarp lenticular-ovoid or rhomboid, reticulate 12
b Endocarp ovoid-acuminate, globose, reticulate or smooth 3
3 a Endocarp ovoid, reticulate, smooth or semi rough, various colours 4
b Endocarp globose to elliptic, quite rough and sunken and raised reticular, white ....***C. adolfi-friderici***
4 a Endocarp smooth, white or cream 5
b Endocarp reticulate with raised boundaries or lines, grey 8
5 a Endocarp smooth, hardly a few boundaries visible, apex rounded 6
b Endocarp smooth not so much and apex beaked 7
6 a Endocarp with a few boundaries, these not raised .... ***C. malagasica***
b Endocarp without boundaries .... ***C. philippensis***
7 a Endocarp smooth not so much, apex rounded .... ***C. prantlii***
b Endocarp rough, apex beaked .... ***C. australiensis***
8 a Endocarp with raised lines and boundaries 9
b Endocarp polygonal, without raised lines 10
9 a Endocarp grey .... ***C. toka***
b Endocarp white .... ***C. bifida***
10 a Endocarp sunken polygonal .... ***C. wightii***
b Endocarp raised polygonal 11
11 a Endocarp white, 6 x 6 x 5 mm .... ***C. australis***
b Endocarp grey, 5 x 4 x 4 mm .... ***C. zenkeri***
12 a Endocarp two-sided 13
b Endocarp four-sided .... ***C. mildbraedii***
13 a Endocarp more than 10 mm long, brown, apex beaked .... ***C. tessmannii***
b Endocarp less than 10 mm long, grey, apex rounded .... ***C. africana***

Endocarp colour

The colours of endocarp are diagnostic and of systematic interest among African *Celtis*. A white endocarp is seen in *Celtis adolfi-friderici, C. bifida, C. prantlii,* and *C. wightii*, while a grey colour is seen in *C. africana, C. australis,* and *C. mildbraedii*. *Celtis gomphophylla* has a dark brown endocarp; it is light brown in *C. tessmannii*, while *C. zenkeri* has cream-coloured endocarp.

Ridges

The presence/absence of a ridge on the endocarp is a significant character in African *Celtis*. There are no ridges in *Celtis philippensis*, there is one main ridge in *C. africana, C. gomphophylla, C. mildbraedii, C. prantlii, C. toka, C. zenkeri, C. wightii* and a few ridges can be seen in *C. tessmannii* and *C. adolfi-friderici* (Table 6.2).

Endocarp sculpture (ornamentation)

Endocarps of African *Celtis* species often have a polygonal sculpture. This structure is formed by the ridges and cross-connection between the edges. Polygonal sculpture is found in *Celtis adolfi-friderici, C. africana, C. australis, C. toka, C. tessmannii, C. bifida,* and *C. mildbraedii*, and normally the surface is rough, especially in *C. tessmannii* and *C. adolfi-friderici*, and the polygones are curved. A non-polygonal shape is found in *C. gomphophylla*, but there are some prominent edges from the bottom. *C. philippensis* has also a non-polygonal shape and smooth surface (Fig. 6.1).

In some species the apex is conspicuously pitted: in *C. adolfi-friderici*, *C. gomphophylla,* and *C. tessmannii* (Fig. 6.1).

With high magnification the outer walls of the endocarp or periclinal walls can be seen to differ. There are two main types. One type of endocarp has rough layers with different sizes of holes, prominent sculpturing, and membranous platelets, while the other one is smooth-layered and fissured, it looks like films in different layers, smooth layers and crusts, and the coverings are usually continuous without very prominent surface sculpturing (Table 6.3).

Table 6.3. Description of endocarp surface (shape of outer layer of the endocarp) of selected species, shown on the SEM photographs of Fig. 6.1.

Taxon	**Description SEM**
C. adolfi-friderici	Rough layers with different size of holes, prominent surface sculpturing, membranous platelets present
C. africana	Smooth layers and fissured layers
C. australis	Rough surface, with a few holes, membranous platelets present
C. mildbraedii	Smooth layers and crusts, continuous coverings usually without very prominent surface
C. tessmannii	Rough layers with holes, prominent surface sculpturing, membranous platelets present
C. wightii	Rough layers with different holes, prominent surface sculpturing

6.4 Discussion

Endocarp characters prove to be important to distinguish species of African *Celtis* in Ulmaceae/Celtidaceae. The endocarp shape varies from elliptic to ovoid, lenticular, or ovoid-beaked. The size of endocarp ranges from small (4 x 3 x 2 mm) to large (11 x 10 x 8) and is very useful in terms of identification of species. The endocarp colour varies from white, cream, and grey to brown and helps to separate species. The endocarp shape varies from globular to polygonal. The outer layers of the endocarp differ; they curve, and are raised from the bottom to the top but in different directions. The apex of the endocarp is round or beaked. The ridges of the endocarp are another character; from a faint ridge to 1-3 clear ridges can be seen among African *Celtis*. Outer layers of the endocarp (sculpture) vary from smooth with different size of holes, to a prominent rough surface, and membranous platelets can be present. The ratio of D/L endocarp length also varies from 3/4 to 6/8. For more details of the species see Table 6.2.

Chapter 7

REVISION OF AFRICAN *CELTIS* (CELTIDACEAE)

A. SATTARIAN, L. J. G. VAN DER MAESEN & J. J. WIERINGA

Two new species have been described in Blumea 50 (2005) 499-503

Summary

In the flora of Africa, Celtidaceae Link is a small family with the main genus *Celtis*. The species, which are mostly trees, are found in tropical and temperate regions of the world. *Celtis* was reported to be represented by c. 8 species in tropical Africa but this study showed that 12 species can be distinguished. *Celtis* species range from North Africa (Algeria, Libya and Morocco) to South Africa and Madagascar. In this investigation two new species were found, one from Madagascar and another from Australia. A key for African *Celtis* is provided, followed by descriptions and distribution maps of the species.

7.1 Introduction

The present chapter is an alpha-taxonomic revision of the *Celtis* species occurring in Africa. The history of the genus and the relationships to other genera have been treated in Chapter 1, molecular support for the species is given in Chapters 2 & 3. The morphology is detailed in Chapters 4, 5 and 6. The herbarium material was obtained on loan and inspected morphologically in the Wageningen Herbarium. Most type specimens could be traced. Many more herbarium sheets were available than have been possible to study in previous treatments, presenting more details of the variation in and the distribution of *Celtis* spp. in Africa. As syntype material was not abundant, we decided in most cases not to select lectotypes.

Celtis L. Sp. Pl. 1043 (1753); Gen. Pl. ed. 5 (1754) 467; *Solenostigma* Endl. Prod. Fl. Norf. (1833) 41; Planch. in DC., Prodr. 17 (1837); Planch., Ann. Sc. Nat. III, 10 (1848) 262; Blume, Mus. Bot. 2 (1856) 70; Miq. Fl. Ind. Bat. 1, 2 (1859) 220; Benth. & Hook.f., Gen. Pl. 3(1880) 354; Engl. & Prantl, Nat. Pflanzenfam. 3, 1 (1888) 63; Bernard, Bull. Herb. Boiss. II, 5(1905) 1112, maps 9-15; J. J. Smith in K. & V. Bijdr. 12 (1910); Leroy, Fl. Madag. et Com. Fam. 54 (1952) 3; Polhill, Kew Bull. 19 (1964) 139; Polhill, Fl. Trop. East Afr. (1966) 3; Hutch. Gen. Fl. Pl. 2 (1967) 147; Letouzey, Fl. Cam. 8 (1968) 6; Elias, J. Arn. Arb. 51 (1970) 32; Soepadmo in Whitmore, Tree Fl. Mal. 2 (1973) 414; Keay et al. Nig. Trees (1989) 282.

Small to large trees, monoecious, deciduous or evergreen, often buttressed. Bark smooth or finely fissured. Branches unarmed, initially densely brown or rufous-hairy, glabrescent, hairs one-celled to multiple-celled, winter buds with scales or not. Stipules thick, peltately attached or free, caducous. Leaves alternate, entire or serrate, 3-veined from base. Inflorescences racemes, panicles or clustered cymelets. Flowers unisexual and bisexual (male and hermaphrodite flowers). Tepals 5-6, basally slightly connate, caducous, stamens equal in number to tepals and glabrous, filaments sublate, incurved in bud and spreading elastically, stigmas 2-armed, bifid. Ovary unilocular, ovoid-ellipsoid. Fruit a drupe, ovoid, ellipsoid or globose, exocarp thick, mesocarp fleshy, endocarp hard, smooth or ridged and pitted. Endocarp scanty or lacking, embryo curved, cotyledons broad.

About 60-100 spp. The species, which are mostly trees, are found in both tropical and temperate regions of the world. Some species of the family are ornamental; some are used for timber and reforestation. *Celtis* was known to be represented by c. 8 species in tropical Africa (Letouzey 1972) but in our present research 12 species (Sattarian & van der Maesen 2005) have been distinguished. *Celtis* species range from North Africa (Algeria, Libya and Morocco) to South Africa and Madagascar. The species are found in different ecological settings. Several tree species are found in the rain forest (*Celtis tessmannii, C. mildbraedii)*; some occur in semi-deciduous forest (*Celtis adolfi-friderici, C. prantlii, C. zenkeri*). Other *Celtis* are shrubs or small trees of rain forest undergrowth (*C. gomphophylla*), or found on the forest/savannah boundary, sometimes in mountain forest (*C. africana*). One species, (*C. toka*), is a fairly large tree with a compact crown, living in savannahs beside streams or planted in villages in the Sudano-Sahelian zone

Key to African *Celtis* based on morphology

1a. Leaves entire, or sometimes serrate at the top (e.g. in water shoots) **2**
1b. Leaves serrate, or at least 1/3 of the margin serrate **9**

2a. Leaves lanceolate, apex acuminate or aristate **3**
2b. Leaves elliptic or cordate, apex caudate or cuspidate **4**

3a. Leaves rounded at base, apex acuminate, smooth hairy,
endocarp polygonal, ovoid, rough, white, only in Madagascar .... **4. *C. bifida***
3b. Leaves not rounded at base, apex aristate, hairs just on veins,
endocarp not polygonal, angular, brown, Africa and Madagascar ..... **5. *C. gomphophylla***

4a. Leaves densely hairy, smooth or rough hairs,
basal main nerves only extending to lower half of leaf **5**
4b. Leaves not densely hairy,
basal main nerves extending to upper half of leaf **7**

5a. Leaves unequally elliptic, or cordate and oblique, third veins not parallel,
rough hairs on both sides, apex cuspidate **6**
5b. Leaves oblanceolate, third veins parallel,
smooth hairs on lower side, apex mucronate .... **12. *C. zenkeri***

6a. Leaves unequally elliptic, oblique at base, apex cuspidate,
endocarp lenticular, polygonal, brown, rough, in rain forest area .... **9. *C. tessmannii***
6b. Leaves cordate to ovate, asymmetric at base, apex acuminate,
endocarp ovoid, polygonal, grey, rough, not in rain forest area .... **10. *C. toka***

7a. Leaves large, 12 x 8 cm, hairs rough (scabrous), fruit 13 x 8 mm, apex caudate or cuspidate,
endocarp globose, reticulations sunken and raised .... **1. *C. adolfi-friderici***
7b. Leaves smaller, a few hairs on main venation, fruit 8 x 6 mm, apex rounded or acuminate,
endocarp ovoid-acuminate or rhomboid, reticulation not sunken and raised so much **8**

8a. Leaves very leathery, no hairs on the venation, apex rounded or shortly acuminate,
fruit 12 x 10 mm, endocarp 10 x 8 mm, only in Madagascar .... **6. *C. malagasica***
8b. Leaves leathery, with a few hairs on the venation, apex mucronate,
fruit 10 x 7 mm, endocarp 8 x 6 mm, East Africa, Asia .... **11. *C. wightii***

9a. Leaf margins serrate except towards the base, leaves cordate to elliptic,
lateral main nerves extending to 1/3 from the base, ... **10**

9b. Leaf margins for 1/3 irregularly serrate, leaves obovate to oblanceolate,
lateral main nerves extending up to half of the leaf **11**

10a. Sepals 6, petiole more than 5 mm long, apex cuspidate, lower leaves smoothly hairy,
endocarp ovoid, white, in Africa only north of the Sahara .... **3. *C. australis***

10b. Sepals 5, petiole less than 5 mm long, apex caudate, in open areas and savannah,
endocarp lenticular, ovoid, grey .... **2. *C. africana***

11a. Leaves oblanceolate, lateral main nerves extending to half of the leaf,
apex caudate, 7 mm long, endocarp ovoid, polygonal, smooth .... **8. *C. prantlii***

11b. Leaves obovate, oblique to cuneate at base, lateral nerves extending to 1/3 of the leaf,
apex cuspidate, 6 mm long, endocarp rhomboid, polygonal, rough ...... **7. *C. mildbraedii***

1. *Celtis adolfi-friderici* Engl.

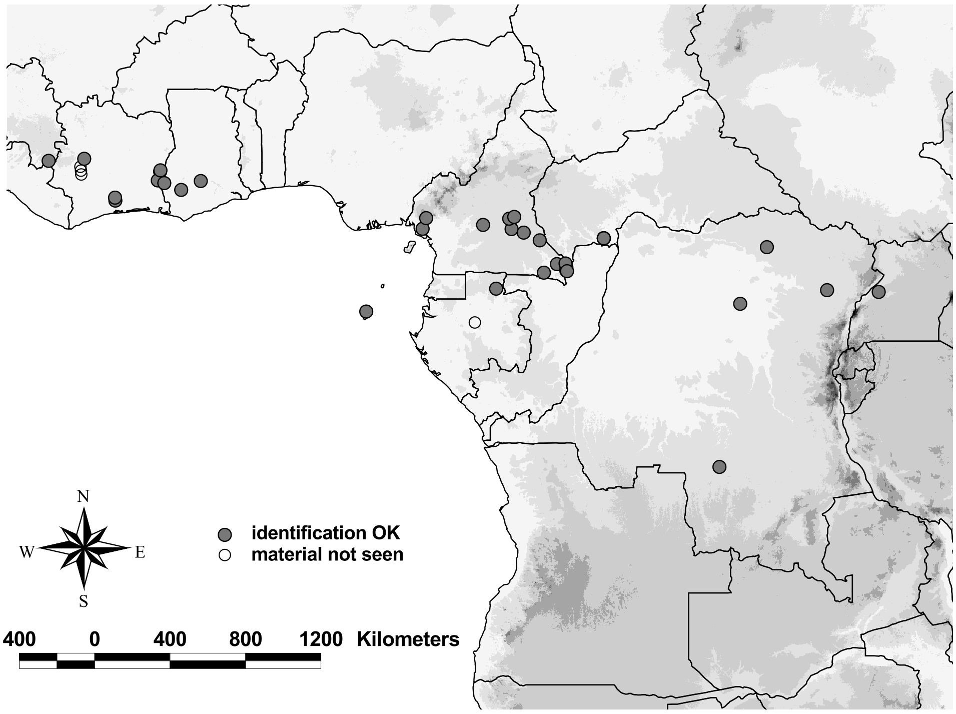
Bot. Jahrb. Syst. 43 (1909) 308 & Mildbraed, Wiss. Ergeb. deutsch. Zentr-Afr. Exped. (1911) 179, t. 16A-D; Engl., Pflanzenw. Afr. 3, 1 (1915) 14; Rendle in Fl. Trop. Afr. 6, 2 (1916) 9; Hauman in Fl. Congo-belge 1 (1948) 44; Dale & Eggeling, Indig. Trees Uganda ed. 2 (1952) 430, fig. 89a; Andrews, Flow. Pl. Anglo-Egypt. Sudan 2 (1952) 253; Fl. W. Trop. Afr. ed. 2, 1 (1958) 529; Polhill, Kew Bull. 19 (1964) 143. Type: Congo Republic, Kivu Province, near Ruwenzori, *Mildbread 2725,* Muera forest *2169 & 2242* (all B, syn!).

Synonyms: *Celtis fragifera* A. Chev. in Bull. Soc. Bot. France 61, Mém. 8e (1917) 299. Type: Ivory Coast, *Chevalier 22575* (isotype; K); *C. ituriensis* De Wild. in Rev. Zool. Bot. Afr. suppl. Bot: 4 (1921). Type: Congo Republic, *Bequaert 2153* (holo: BR).

Tree 20-35 m tall, semi-deciduous, monoecious, trunk with buttresses, twigs pubescent, leaf-blades entire, alternate, oblong-elliptic, 10-16 cm long, 5-8 cm wide, shortly acuminate, rounded and unequal-sided at base, 3-nerved from the base, with the basal lateral nerves extending almost to the apex and upper prominent lateral nerves 1-2 on each side of the midrib, petiole 5-18 mm long. Stipules small, 3 mm long, shortly produced below the point of attachment, pubescent, caducous. Cymes 1-4 cm long, long in flower, up to 6 cm in fruit, at the nodes below, lower ones with many clustered male flowers, upper ones with several hermaphrodite at the top. Sepals 5-6, 1-1.5 mm long, pubescent.Ovary pubescent with a ring of longer hairs at the base, styles branched, 3-4 mm long. Fruit a drupe, ovoid to obovoid, 15-20 mm long, 13-15 mm wide, red to black (at maturity), endocarp 10 x 9 mm, ellipsoid, polygonal, rough. Pollen grains triporate, spheroidal.

Distribution: Liberia to Uganda and Congo-Kinshasa. (map 7.1).
Habitat and ecology: Lowland rain forest (100-600m).

Specimens examined:
***Celtis adolfi-friderici* Engl.**
CAMEROON: **Central Province**: c. 115 km NE of Yaoundé [Jaunde], transition zone and warzone [Kampfgebiet] opposite of the savanna on the Northern border of the Hylaea, south of the Sanaga between Yaoundé and Dengdeng, not far from confluent of Lom (Sanaga) and Djerem, February 1914, *Mildbread, G.W.J. 8250* (K); **East Province**: 27 km SW of Bertoua, road to Doumé, S of Dimako, near Toungrélo, 9 January 1962, *Breteler, F.J. 2456* (A, BR, FI, K, LISC, M, P, UC, WAG, YA); 50 km W of Béla (along Sangha R., near C.A.R. border, about 82 km E of Lokomo, 2 December 1982, *Kruif, A.P.M. de 804* (WAG); About 30 km NW of Moloundou, 7 December 1982, *Kruif, A.P.M. de 865* (WAG); 10 km N of Ndemba II = 30 km N of km 29 of road Bertoua-Nanga Eboko, 12 June 1965, *Leeuwenberg, A.J.M. 5843*



Distribution map 7.1. *Celtis adolfi-friderici* in Africa.

(BR, K, P, WAG); Piste forestière Letta - Viali feuille IGN-1/200.000 Bertoua, 9 February 1960, *Letouzey, R. 2999* (P); 32 km WNW of Mopwo (village) km 22 of road Yokadouma-Batouri, 6 June 1963, *Letouzey, R. 5244* (P); S Cameroon forest area molinde mouth of the Bok river in Bimba, 13 July 1911, *Mildbread, G.W.J. 4239* (WAG); **South-West Province**: Victoria District, between Bafia and Likoko, in disturbed lowland rain forest and volcanic lava, 5 February 1958, *Keay, R.W.J. FHI 37522* (FHI, K, P); Secondary forest at Bolo-Meboka, Kumba-Mamfe road, 4 July 1987, *Thomas, D.W. 7157* (MO);

CENTRAL AFRICAN REPUBLIC: **Lobaye**: Station of Boukoko, 10 February 1953, *Tisserant, C. 2451* (P); Station of Boukoko, 10 February 1953, *Tisserant, C., Equipe 245* (P); Bounkoko, 4 November 1947, *Tisserant, C., Equipe 429* (P); Station of Boukoko, 27 June 1950, *Tisserant, C., Equipe 1788* (G, P); Station of Boukoko, 6 October 1951, *Tisserant, C., Equipe 2065* (P); station of Boukoko, 10 February 1953, *Tisserant, C., Equipe 2451* (P, WAG); Region of Mbaiki, Station center of Boukoko, 23 February 1953, *Tisserant, C., Equipe 2463* (G, P); **Sangha**: Boa tribs, North F.R., 20 February 1971, *Hall, J.B. 42653* (MO); **Sangha Economique**: Lindjombo, within 3 km of village, 15 November 1988, *Fay, J.M. 8834* (MO); 45 km south of Lidjombo, Ndakan gorilla study area, 10 December 1988, *Harris, D.J. 1671* (MO); 45 km S of Lidjombo, Ndakan gorilla study area, 13 February 1989, *Harris, D.J. 1851* (MO, WAG); **Unknown**: Ndakan gorilla study area, 5 February 1988, *Fay, J.M. 8216* (MO, WAG);

CONGO (BRAZZAVILLE): **Sangha**: Sangha-Bois, chantier of Mangokele. 15km from Ngoko (Cameroonian river), 23 July 1965, *Bouquet, A. 1638* (P);

CONGO (KINSHASA): **Kasai Oriental**: Mwene Ditu, 14 February 1950, *Hardy, D.S. 48* (BR, MO, YBI); **Orientale**: Bambeto 1942, *Dubois, H. 658* (BR, YBI); Yangambi, 1949, *Germain, R. 744* (BM); zone de Mambasa (Ituri), 4 March 1982, *Hart, T.B. 216* (BR, WAG);

GABON: **Ogooué-Ivindo**: Réserve de la Lopé près du Centre d'études des gorilles et chimpanzé (CEGC), 19 July 1993, *Lejoly, J. 93/ 172* (BRLU; not seen!); **Woleu-Ntem**: Minkébé area, 1000 m from the camp, 23 March 1990, *Minkébé Series AM 55* (WAG);

GHANA: **Ashanti Region**: Ashanti, Sekyere, 5 October 1988, *Kisseadoo, S. 26* (NY); **Western Region**: BIA, National Park and Producation, Reserve ca. 7km south of Sefwi-Adjoafua. Along timber access road, travelling south from Adjoafua, Park Guard camp, 28 February 1996, *Schmidt, H.H. 1995* (MO); Anwhiaso Reserve, March 1927, *Vigne, C. 270* (NY);

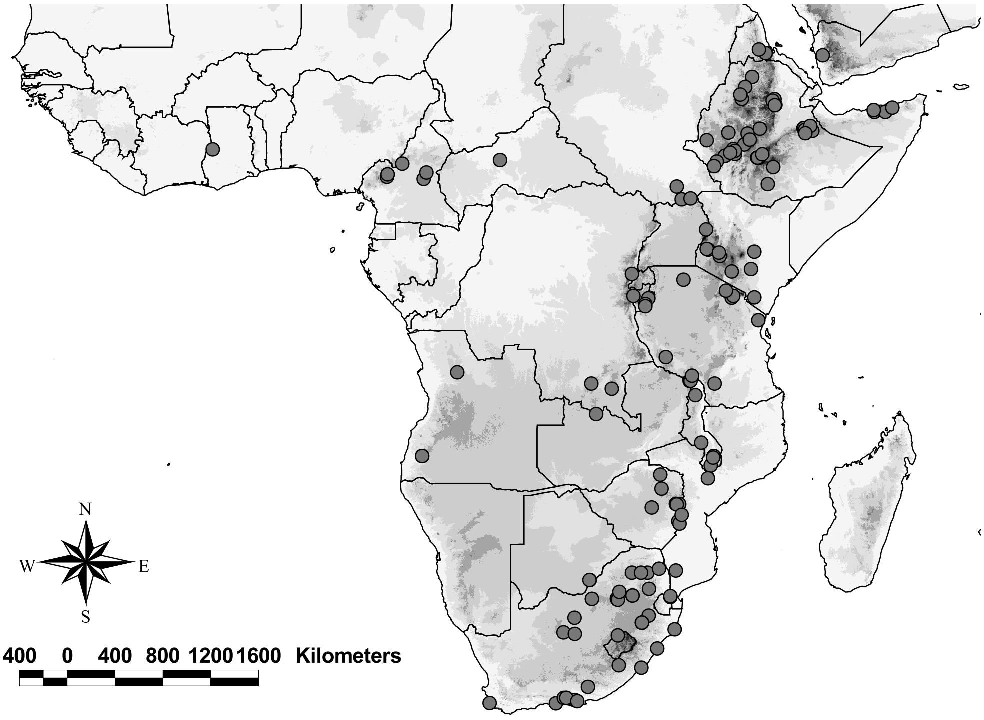
IVORY COAST: **Abengourou**: 25 km east of Abengourou, along the road to Niable, 31 July 1969, *Versteegh, C. 610* (WAG); **Agnibilékrou**: Vallée du Moyen Comoé, entre Tingouéla et Assikasso, 14 December 1909, *Chevalier, A. 22575* (P, WAG); c.10 km N of Agnibilekrou; c. 250 km NE of Abidjan, 20 August 1963, *Wilde, W.J.J.O. de 687* (P, WAG); **Daloa**: F.C. du Haut-Sassandra, Sud forêt, piste de V12, layon 27, 14 February 1994, *Kouamé, F.N. 1104* (CSRS; not seen!); **Divo**: N-W forêt de la Boubo. Ouest du village V3 de palme-industrie, 11 December 1990, *Chatelain, C. 576* (G); Surroundings of IFCC, 10 km south east of Divo, 7 July 1969, *Versteegh, C. 412* (WAG); **Man**: F.C. Scio, Pinhou, Lobykro à 9 km, Bloc 28 Parcelle 139 de la Sodefor, forêt en bordure de piste principale, 18 August

2001, *Nusbaumer, L. 493* (G, WAG); **Unknown**: 1932, *Aubréville, A. (Ivory Coast series) 986* (WAG); **Vavoua**: F.C. du Haut-Sassandra, Centre. Forêt peu dégradée, relevé FNK24, 18 August 1994, *Kouamé, F.N. 1341* (CSRS; not seen!); F.C. du Haut-Sassandra, Nord. bord de piste, layon 13, 31 August 1995, *Kouamé, F.N. 1554* (CSRS; not seen!);
LIBERIA: **Nimba**: Yéképa, 29 September 1975, *Adam, J.G. 29655* (MO, WAG);
SAO TOMÉ AND PRINCIPE: **Sao Tomé Island**: N Coast, Praya das Conchas, about 1 km from the ocean shore, 26 January 1980, *Wilde, J.J.F.E. de; Arends, J.C.; Groenendijk, L. 302* (FR, STOME, WAG);
UGANDA: **Western Province**: Bunyoro, W Bugoma, Bugatiya county, 13 October 1962, *Styles, B.T. 135* (FHO, K).

2. *Celtis africana* Burm. f.

Prodr. Fl. Cap. (1768) 31; Rendle in Fl. Trop. Afr. 6, 2 (1916) 3; Hauman in Fl. Congo-belge 1 (1948) 43; Keay in Fl. W. Trop. Afr. ed. 2, 1 (1958) 592; F. White, F.F.N.R. (1962) 22; Polhill, Kew Bull. 19 (1964) 139; von Breitenbach, Indig. Trees Southern Afr. 2 (1965) 79, t. on p. 81; Polhill in F.T.E.A., Ulmaceae: 4 (1966); Letouzey in Fl. Cameroun 8 (1968) 14, t. 1 fig. 3; Jacot Guillarmod, Fl. Lesotho (1971) 161; Palmer & Pitman, Trees S. Afr. 1 (1972) 423, t. & photos; K. Coates Palgrave, Trees Southern Africa (1977) 96, fig. 16; Beentje, Kenya Trees, Shrubs & Lianas (1994) 318. Type: S. Africa (pl. 88 in Burm. 1768).

Synonyms:
Celtis eriantha E. Mey. ex Planch., in Drege, Flora 26, Bes. Beigabe (1843): 171 (1844), nom. nud.; *C. kraussiana* Bernh., Flora 28 (1845) 87. Type: South Africa, *Krauss* (G, isotype); *C. burmannii* Planch., Ann. Sc. Nat., sér. 3, 10 (1848) 296. Type: South Africa, *Drege* (K, isolecotype); *C. opegrapha* Planch., Ann. Sc. Nat. sér. 3. 10 (1848) 294. Type: South Africa, Cape prov., Drege 8261b (K, isolecotype); *C. henriquesii* Engl., Notizbl. Bot. Gart. Berlin 3 (1900) 22. Type: Angola, *Welwitsch* 6308 (BM, K, isolecotypes!); *C. vesiculosa* Hochst. ex Planch., Fl. Col. Eritrea (1903) 119. Type: Ethiopia, *Schimper 1162* (BM, K, isotypes); *C. holtzii* Engl., Pflanzenw. Afr. 3 (1) (1915) 12, fig. 6E. Type: Tanganyika, *Holtz* 1591 (B, holotype!); *C. kraussiana* var. *stolzii* Peter, Feddes Repert. Beih. 40, 2 (1932) 64. Type: Tanganyika, *Stolz* 1708 (B, holotype!; BM, K, isotype!);



Distribution map 7.2. *Celtis africana* in Africa.

Tree, 10-25 m tall, deciduous, monoecious, bole slightly fluted, bark smooth, whitish-grey often pinkish-blotched, fresh cut wood unpleasant-smelling. Young stems and branches densely tawny pubescent-tomentose, leaf blades coarsely dentate-serrate, ovate to ovate-lanceolate, alternate, 3–9 cm long, 2.5–5.5 cm wide (juvenile leaves up to 13 x 7) cm, apex acuminate, base rounded to cuneate and strongly asymmetrical, lamina thinly or thickly chartaceous, ± scabrous, young foliage often densely tawny-pubescent on both sides, later glabrescent except on nerves below, 3-nerved from the base, basal lateral nerves extending well into upper half, upper lateral nerves 1–2 on each side of the midrib, all lateral nerves prominent below; petiole 2–5 (10) mm long. Stipules linear to linear-obovate, 3–8 mm long, pubescent, Inflorescences precocious, those cymes borne in the lower leaf axils and at the nodes below contain 3-many clustered male flowers on pedicels 1.5–5 mm long, the cymes borne in the uppermost leaf axils contain 1-several bisexual flowers on pedicels 10–17 mm long, intermediate cymules consisting of both male and bisexual flowers, axis and pedicels usually densely tawny-pubescent, sepals 4–5, 1.5–2.5 mm long, Ovary densely pubescent, styles unbranched 1.5–3.5 mm long. Fruit a drupe, subglobose, less often ovoid- ellipsoid, 5-7 mm long, 3-6 mm wide, orange or black, endocarp 4x3 mm, ovoid, reticular (polygonal), gray. Pollen grains triporate, oblate spheroidal.

Distribution: widespread from Sudan, Nigeria, South Africa (map 7.2).
Habitat and ecology: Savana, dry evergreen forest, upland rain forest (400-2000 m).

Specimens examined:
***Celtis africana* Burm.f.**
ANGOLA: **Unknown**: Cazengo, Granja, *Gossweiler, J. 6488* (C);
BOTSWANA: Gaberones (District), 11 December 1961, *Yalala, A.M. 152* (CAH, MO);
BURUNDI: **Ruyigi**: Mosse-Ruyigi, Kiofi, plot 5 section I, 18 September 1951, *Michel, G. 364* (BR, MO); Ruyigi, Nyakazu gouffre, January 1973, *Reekmans, M. 2735* (MO); Nyakazu, 24 September 1980, *Reekmans, M. 9458* (MO);
CAMEROON: **East Province**: Mont Tamber, Deng-Deng, 16 February 1961, *Letouzey, R. 3475* (P, WAG); **North Province**: 23 km East south of Bagodo, Eastern top of Kaia Dangano, 4 August 1966, *Letouzey, R. 7651* (P); near Kori, 50 km SW of Banyo, 24 June 1974, *Letouzey, R. 8715* (P); **Unknown**: 1946, *Aubréville, A. 597* (P); **West Province**: 25 km W of Foumban, 28 October 1974, *Letouzey, R. 13045* (P); Mbam Massif, West slope, direct path from Nkoutoupi to the top (35 km NW of Foumban), 31 October 1974, *Letouzey, R. 13070* (P); Mbam Massif, West slope, direct path from Nkoutoupi to the top (35km NW of Foumban), 31 October 1974, *Letouzey, R. 13074* (WAG);
CENTRAL AFRICAN REPUBLIC: **Gribingui**: Kago Bandoro (=Fort Crampel), June 1960, *Guigonis, G. 1863* (P); **Ouaka**: region de la Ouaka, 12 February 1926, *Tisserant, C. 1831* (WAG);
CONGO (KINSHASA): **Katanga (Shaba)**: Kayo, waterfall of Kalule Nord, 29 January 1986, *Bamps, P. 8376* (BR, WAG); plateau of Kundelungu, 23 km WSW of the station of Dualale, 1 km to the right of the Kaloba falls, 7 January 1970, *Lisowski, S.; Malaisse, F.; Symoens, J.-J. 9244* (BR); **Nord-Kivu**: Park Nat. Albert, between Muguga and the Rumoka river, November 1937, *Lebrun, J. 8583* (BR, COI); **Sud-Kivu**: 162 km on road to Uvira and Mbaraka, Ruzizi plain, May 1950, *Germain, R. 7029* (BM);
ERITREA: **Unknown**: Amasen, Bet-Garghis, lungo un torrente che scende da S. Giorgio a valle Makalo, 5 February 1902, *Pappi, A. 2708* (COI, G, NY); Valley of Marakhãt, Saganeïti, 10 April 1892, *Schweinfurth, G. 1697* (BR, G); Vally of Marakhãt, Saganeïti, 17 April 1892, *Schweinfurth, G. 1717* (G);
ETHIOPIA: **Arsi**: c. 5 km from Degaga, 21 February 1970, *Gilbert, M.G. 1763* (K); 8 km S of Shashemene, 5 February 1965, *Perdue, R.E. 6482* (K); **Bale**: Bale A. Region: c. 14 km N of Dolo Menna (Masslo) on the road to Goba, 26 October 1984, *Friis, I. 3491* (C, K); **Gojam**: Bahir Dar, shore of Tana Lake, 28 September 2003, *Wieringa, J.J. 4931* (ETH, WAG); Bahir Dar, shore of Tana Lake, 28 September 2003, *Wieringa, J.J. 4932* (ETH, MO, WAG); **Gondar**: between Gondar and lake Tana; at river near the village of Wusaba, 21 July 1988, *Friis, I. 5361* (C); Isola Daga, 22 February 1937, *Pichi Sermolli, R.E.G. 1681* (MO, WAG); **Harerge**: Campus Agric.College Alemaya,HSIU, 1 April 1974, *Bos, J.J. 7586* (ACD, WAG); Rocky valley, between Errer and Dakata valley on the Harar-Jijiga road, 1 June 1974, *Bos, J.J. 7851* (WAG); near College of Agriculture, Alemaya, along road to Awalle, 24 February 1976, *Jansen, P.C.M. 5183* (ACD, WAG); around Bati village, 5 March 1976, *Jansen, P.C.M. 5208* (ACD, WAG); 35 km NW of Jijiga, 1-4 km W of Giri Kocher, 13 November 1976, *Le Houérou, N.-H. 131176/01- 2* (FT); Fruit farm Mrs. Diggs. 3.5 km from the road from Alemaya to Harar, side road from Hamaressa, 13 July 1967, *Westphal, E. 616* (ACD, BR, C, CAM, DES, EA, MO, WAG); road from Shashamane-Koffale, 10km from Shashamane, 7 September 1967, *Westphal, E. 1713* (ACD, BR, C, MO, WAG); 3 km on the road from Harrar to Jijigga, 10km from the main road, near Mederu village, 21 October 1967, *Westphal, E. 2326* (ACD, BR, C, CAIM, MO, WAG); c. 9 km from Harar on the road to

Jijiga, near the village of Harrewé, 20 December 1968, *Wilde, J.J.F.E. de 4271* (ADC, B, BR, C, LMU, MO, WAG); "Rock Valley", about 36 km along the road from Harrar to Jijiga, 12 February 1970, *Wilde, J.J.F.E. de 6341* (ACD, BR, M, MO, WAG); c 10 km SE of Harrar, 31 January 1966, *Wilde, W.J.J.O. de 9845* (B, BR, C, K, MO, P, PRE, WAG); **Harrar**: Amaressa near Diggs farm +/- 5 km NNW of Harrar, 28 February 1963, *Willan, R.G.N. 2587* (US); **Kaffa**: Badda Buna Forest, 10 km NE of Jimma, 21 November 1961, *Meyer, F.G. 7768* (K, US); **Kefa**: Kefa A.Region. At the Bebeka Coffee Plantation, S of Mezan Tefari. Near the H.Q., 2 December 1984, *Friis, I. 3952* (C, K); Kefa A. region: At Bebeka coffee Plantation, south of Mezan Tefari, near the H.Q., 2 December 1984, *Friis, I. 3953* (C, K); Kaffa Prov. 1.5 km NW of Aro along the road between Jimma and Agaro, 7 November 1970, *Friis, I.; Hounde, A.; Jacobsen, K. 156* (C, WAG); c. 20 km SW of Jimma on Bonga road, 10 November 1970, *Friis, I.; Hounde, A.; Jacobsen, K. 243* (C, WAG); Wush-wush (small village near Bonga) near tea plantation of H.V.A., 23 March 1976, *Jansen, P.C.M. 5473* (ACD, WAG); Wush-wush (small village near Bonga) near tea plantation of H.V.A., 23 March 1976, *Jansen, P.C.M. 5491* (ACD, WAG); Jimma road, c 10 km SW of bridge over Omo river, 28 February 1966, *Wilde, W.J.J.O. de 10271* (B, BR, C, K, MO, P, PRE, WAG); **Shewa**: 45 km NW of Addis Ababa, off the Bahar -dar-Gondar road, 5 February 1972, *Ash, J.W. 1539* (K); along road from Shashamane to Mendo, c. 8 km from Shashamane, 25 June 1976, *Jansen, P.C.M. 6646* (ACD, WAG); c. 4 km W of Ambo, about 125 km W of Addis Ababa, 29 April 1965, *Wilde, W.J.J.O. de 6458* (B, BR, C, ETH, K, MO, WAG); c. 15 km SE of Shashamane, 15 June 1965, *Wilde, W.J.J.O. de 7040* (BR, C, ETH, K, MO, WAG); c 20 km W of Lekemti, 2 July 1965, *Wilde, W.J.J.O. de 7222* (B, BR, C, ETH, H, K, MO, WAG); **Shoa**: 106 km SW of Addis -Ababa,on Jimma road, 26 May 1973, *Ash, J.W. 1963* (MO, WAG); **Unknown**: Dissected plateau, lavas, humus-rich forest, Matakome (Galle). Agheremariam, 3 December 1952, *Gillett, J.B. 14592* (BM, K); Thlokweng, 18 August 1978, *Hansen, O.J. 3432* (BM, C, WAG); Belletta, 16 November 1943, *Logan, W.E.M. 53* (G); 8 April 1989, *Mesfin Tadesse 7371* (C); 25 km of Uddus Gabriel, 4 November 1937, *Pichi Sermolli, R.E.G. 1685* (BM, MO); in montibus Sementibus, 1842, *Schimper, G.H.W. II: 1162* (BR, WAG); Durrona, 1853, *Schimper, G.H.W. III: 1435* (BR, P, WAG); **Welega**: Humbi forest, Dembi-Dollo, April 1937, *Guigharelli, D. 779* (FT); **Welo**: Tis - Aba-Lima, c. 50 km N of Dessio, 25 October 1987, *Mesfin Tadesse 6303* (C); Kalu Awraja, Cheleka River gorge, ca. 30 [?? number illegible] km SW of Degan, 27 October 1987, *Mesfin Tadesse 6434* (C); Ambasel Awraja Anabe Forest, 28 May 1987, *Mesfin Tadesse 6531* (C); Ambassel Awraja. between Kerkero & Ketetya on the road from Anabe to Gerba 2270-2580 m, 28 May 1987, *Mesfin Tadesse 6564* (C);

GHANA: **Unknown**: Degedege SW Nsawkaw, 29 May 1974, *Hall, J.B. GC 44851* (GC, K);

KENYA: **Coast**: Taita-Taveta District, Ngangao Forest, 16 May 1985, *Faden, R.B. 528* (WAG); **Eastern**: Meru District, Lake Nkunga, 12 April 1985, *Burney, D.A. E 42* (NY); **Nyanza**: North of Nyanza District, Mweyu (Luyia), 7 April 1965, *Gillett, J.B. 16675* (C, WAG); Nyanza Province, north kavirondo Distr., 17 September 1949, *Maas Geesteranus, R.A. 6267* (BR, EA, G); **Unknown**: Ngong Forest, 26 March 1998, *Ahenda, J. 27* (WAG); Kitui district, C. 15 ESE Kitui, Inyuu on Zombe road, 11 January 1988, *Alstrup, V. K 300* (C); Maji Mazuri, 1934, *Angus, T.A. 7117* (NY); Turi area near Molo (Mr Start's Farm), 21 January 1968, *Gillett, J.B. 18518* (WAG); **Western**: Kakamega Forest, forest near the Rest House, 26 December 1969, *Faden, R.B. 69/ 2085* (MO);

LESOTHO: **Leribe district**: Basutoland, district de Léribé, 1911, *Dieterlen, A. 193* (WAG; not seen!);

MALAWI: **Central Province**: District: Dedza, Ngoma, Chongoni Forest, 11 January 1970, *Salubeni, A.J. 1498* (K, MO); **Northern Province**: Misuku, 3 March 1983, *Dowsett-Lemaire, F. 673* (BM, BR); 12 November 1959, *Robson, N.K.B. 579* (BM); **Southern Province**: Thondwe, Mpita tobacco Estate, 2 November 1984, *Balaka, J.L. 757* (MAL, MO); Mpita (A. L.C), Tobacco estate, Reg. Zomba, 1 November 1983, *Patel, I.H. 1310* (MAL, MO, NY); Reg. Zomba Dist. Mpita Estate, Thondwe, 6 November 1984, *Tawakali, E.J. 421* (MAL, MO, NYAS); **Unknown**: Cholo Mountain, Cholo District, 22 September 1946, *Brass, L.J. 17744* (BM, K, MO, NY); Thondwe zomba, 3 May 1982, *Chapman, J.D. 6157* (K); Mpita (A.L.C.) Tobacco estate, Thondwe, Zomba, 7 May 1982, *Chapman, J.D. 6195* (BR); National Park, 12 September 1983, *Dowsett-Lemaire, F. 130* (BR);

MOZAMBIQUE: **Gaza**: 10 km of Chipenha para Mainguelana, floresta Muguaze (Chirrinzene), 28 September 1971, *Correia, M.F. 2264* (LM, WAG); **Maputo**: Namaacha, Monte Ponduini, próximo do posto de rader dos C.T.T. (cp), 28 October 1971, *Marques, A. 2332* (LM, WAG); **Unknown**: near Goba Fronteira on the margin of dunes near the sea, 3 October 1961, *Balsinhas, A. 520* (BM); Lebombo Mountain Range, February 1974, *Tinley, K.L. 3011* (K);

SOMALIA: Somaliland Prot., at Daloh, 18 miles N of Erigavo, 6 November 1954, *Bally, P.R.O. 10346* (G, K, P); Bodar Som. at Daloh, 18 miles N of Erigavo, 6 November 1954, *Bally, P.R.O. 10349* (K); Somaliland, eastern Almadu range, northern slopes, 13 October 1956, *Bally, P.R.O. 11088* (G); near Etigavo (gypsum), 8 February 1945, *Bally, P.R.O. 12852* (G, K); 15 July 1945, *Gillardin, J. 951* (BM); Algasonia, 21 February 1933, *Gillett, J.B. 5098* (K); N Somalia, 7 July 1981, *Gillett, J.B. 23788* (BR); 15 July 1945, *Glover, P.E. 951* (K); Sheikh, 3 May 1973, *Ironside Wood, J.R. S/73 41* (K); Sheikh area, 3 May 1973, *Ironside Wood, J.R. S/73/ 41* (K); Berstje/Bersije, 16 August 1957, *Newbould, J.G.B. 1014* (K, MO);

SOUTH AFRICA: **Cape Province**: Lambeau, Grootbos, 2 February 1982, *Léonard, J.J.G. 7321* (BM); **Eastern Cape**: Beans bush, near Patensie, 12 September 1973, *Bayliss, R.D.A. BRI 532* (BR, P, WAG); Baviaans Kloof, Eastern cape, 29 November 1974, *Bayliss, R.D.A. BRI 1172* (MO); Baviaans kloof, E.cape, 13 September 1974, *Bayliss, R.D.A. BS 6792* (WAG); Baviaans Kloof, 10 November 1974, *Bayliss, R.D.A. 6916* (MO, WAG); c. 20 km NW of Ugie (direct) farm: Copeland. 3128AA, 5 May 1993, *Bester, S.P. 526* (E, PRE); Spreeuwkloof, Cookhouse, December 1969, *Olivier,* *M.C. 381* (MPE, WAG); District: Humansdorp, Gamtoos valley, Near scotts cave, 20 November 1963, *Wells, M.J. 2717* (BR); **Eastern Transvaal**: 18 km from Lydenburg turn off on Lydenburg-Machadodorp Road, Badfontein Farm, opposite Braam Raubenheimer Dam (Kwena Dam), Marantan Hill Trail, 18 April 1997, *Prentice, C.A. 111* (PRE, WAG); **Gauteng**: near Pretoria, 11 April 1962, *Bernardi, L. 9060* (G, US, WAG); Johannesburg, Randburg district, Darren wood koppie on third avenue, Linden. Cresta side of dam, entrance from Danie street 2627BB, 24 September 1997, *Reddy, R.A. 431* (C, MO); Johannesburg, Randburg district, Robindale, Park on the corner of Bellairs street and Gaiety avenue, on serpentine, facing Bellairs street 2627BB, 24 September 1997, *Reddy, R.A. 465* (B, C, PRE); **Kwazulu-Natal**: Weenen district, Tugela river valley, beside the road to Zingela, 16 November 1989, *Balkwill, K. 5078* (B, BRY, E, M, MO, PRE); Natal region, December 1972, *Crook, R.A. 1898* (MO); D. Lerequier's garden, Dunlau, 18 November 1966, *Dahlstrand, K.Å. N 46* (MO); Utrecht dist: Retirement 2730 AD, 4 October 1985, *Devenish, N.J. 1880* (PRE, WAG); Hluluwe Game Reserve, 1 March 1982, *Dickinson, J. 30* (MO); Station Dumisa, 21 August 1910, *Rudatis, A.G.H. 1108* (G, WAG); Karugha, 2 January 1895, *Schlechter, F.R.R. 6160* (BM, G); Durban, Natal, 14 August 1896, *Wood, J.M. 6123* (G); **North West Province**: 8 miles Lichtenburg-Zeerust road, 28 January 1968, *Morris, J.W. 1126* (PRE, WAG); at base of limestone escarpment, west side of Harz River Near Taungs, 75 miles north of Kimberley, 31 January 1948, *Rodin, R.J. 3456* (US); **Northern Cape**: Hay district, 13 miles from Schmidtsdrif to Papkuil, 7 March 1967, *Tölken, H. 1170 A* (BM); **Transkei**: Umsikaba, Ndindini, 10 November 1970, *Strey, R.G. 10106* (NH, WAG); **Transvaal**: 8 February 1960, *Bayliss, R.D.A. 9007* (US); Bryanston. 8 miles N of Johannesburg center, 13 January 1962, *Dahlstrand, K.Å. 579* (C); Lichtenburg (2626AA), Vlakfontein, 10 February 1970, *Morris, J.W. 1127* (E, PRE); c. 9 miles west of Krugersdorp on Farm Gladysvale, 27 February 1948, *Rodin, R.J. 3899* (PEU); Small Kloof, below road to Zulu Bull's village about ½ mile from new dam, Westfalica, 27 September 1960, *Scheepers, J.C. 1007* (MO, PRE, WAG); Region, Transvaal. Dist, Lichtenburg. About 3 miles north of lichtenburg on the Zeerust road, 9 March 1967, *Scheepers, J.C. 1484* (BR); near Selati river, 3 September 1985, *Stalmans, M. 632* (E, PRE); **Unknown**: December 1972, *Crook, R.A. 59831* (E, PRE); Off Monzi road. North of old farm ruins (Dukuduku), 12 December 1989, *Hobson, S.R. 603* (GRA, MO); November 1933, *Meebold, A.K. 12671* (M); 75 km miles north of Kimberley, 31 January 1948, *Rodin, R.J. 3426* (MO, NY); 31 October 18, *Unknown s.n.* (P); **Western Cape**: Knysna (3423 AB), Keurbooms River bridge, 27 September 1967, *Marsh, J.A. 618* (PRE, WAG);

SUDAN: **Eastern Equatoria**: Equatoria prov., 12 May 1939, *Andrews, F.W. 1175* (BR); near Gilo village, 15 November 1980, *Friis, I.; Vollesen, K. 217* (C); Iwowa, Didimga, Lukoi-Oich., 22 April 1939, *Myers, J.G. 11033* (K); **Unknown**: Imatang, 13 February 1976, *Howard, W.J. IM 31* (K);

TANZANIA: **Arusha**: Arusha District, 4 km N of USA River, 10 December 1988, *Pocs, T. 88290 A* (K); Munduli forest Reserve, near Onjoro Ondare village, 21 January 1999, *Simon, G. 91* (C); Ketumbeine Forest Reserve, near Iloriento Village NNE of Losirwa Village, 15 February 2001, *Simon, G. 773* (MO); **Kilimanjaro**: Chome-Suji division, Chome ward, Gwang 'a village, Gonja kisanzuni street, Njokava Sacred Forest, 16 December 2000, *Kindeketa, W. 640* (MO); **Mwanza**: Ukerewe area, February 1929, *Conrads, A.H. 6003* (EA, WAG); **T2 Northern**: Tanganyike, April 1941, *Bally, P.R.O. 2401* (G); **Tanga**: near Wanguwe river, Gare- foothpath, *Shabani, S. 314* (BM);

Unknown: T4, s' Wanga District. Mbizi F.R., 4 November 1987, *Ruffo, C.K. 2644* (C);

UGANDA: Namojongotyang, Debasien, *Eggeling, W.J. 2678* (BR);

UNKNOWN: South-East Africa, 1880, *Nelson, W. 250* (K);

YEMEN: **Al Hudaydah**: Gebel Bura, über Hille, 5 January 1889, *Schweinfurth, G. 457* (G);

ZAMBIA: **North-Western Province**: Solwezi, 26 July 1964, *Fanshawe, D.B. 8848* (K, NDO);

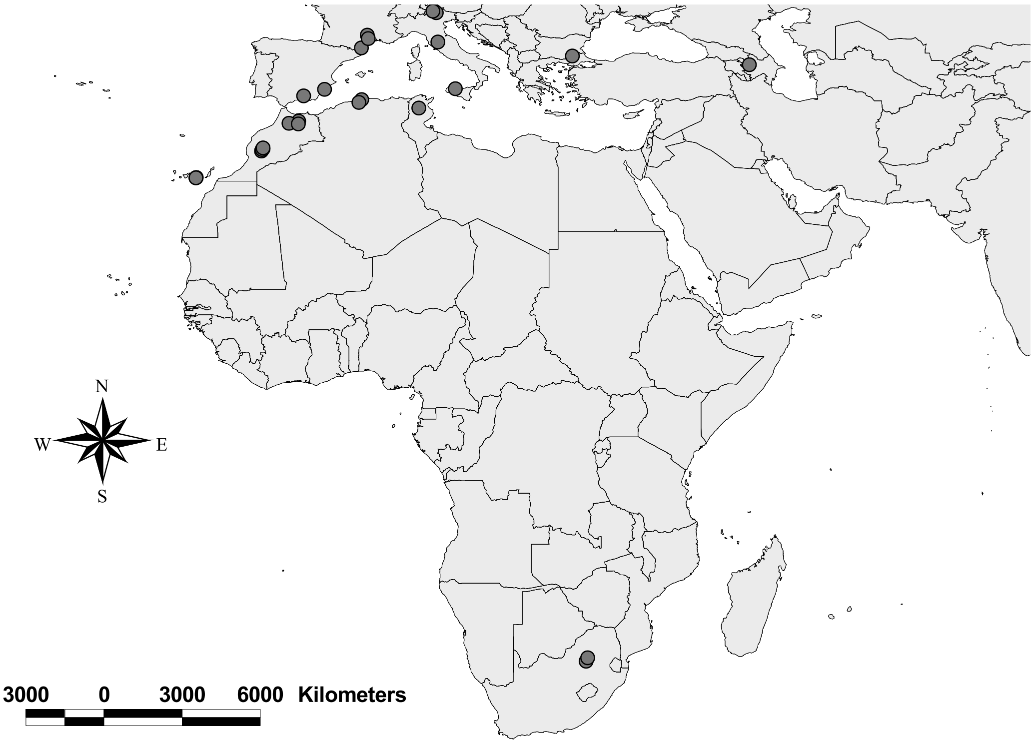
ZIMBABWE: **Chipinga**: District: Chipinga, October 1966, *Goldsmith, B. 66/ 77* (BM, BR); **Manicaland**: District:manicaland, 15 October 1954, *Chase, N.C. 5309* (BM); District: Manicaland, 16 October 1954, *Chase, N.C. 48774* (BR); **Unknown**: Melsetter, Bridal veil Falls, 11 January 1974, *Bamps, P.; Symoens, J.J.; Vanden Berghen, C. 765* (BR, WAG); S.w. of Mlenje Banks of little Odsj River, 17 September 1955, *Chase, N.C. 5793* (CAH); District: Umtali, 4 December 1958, *Chase, N.C. 7012* (BR); From Satsi River, 26 September 1937, *McGregor, G.M. ma5/ 34* (BM); Dist: Chilimanzi, 2 May 1951, *Mylne, M.R. 16/ 51* (MO); Harare, 3 November 1997, *Poilécot, P. 7339* (G); District Chirinda, 18 October 1947, *Wild, H. 2039* (BR, K).

3. *Celtis australis* L.

Sp. Pl. 1043 (1735); Derevya Kustarniki SSSR 2: f. 138, 1 (1951); Hegi, Fl. Mittel-Eur. ed. 2, 3 (1): f. 117 (1958); Fl. Iran. 142: 12 (1979); Fl. Turkey 7 (1982) 650. Lectotype: Herb. Linn. No. 1209.2 (LINN), designated by**:** Zielin'ski, in Rechinger (ed.), Fl. Iranica 142: 12 (1979).

Tree, 10-20 m tall, monoecious, bark grey, smooth. Young twigs velutinous, leaf blades sharply serrate, alternate, ovate-lanceolate to lanceolate, 4-8 cm long and 2-4 cm wide, oblique at base, usually long-acuminate, 3 nerves at base reaching 2/3 of the blade, scabrid above, velutinous and brownish or brownish-green, petiole to 4-8 mm long. Inflorescences precocious cymes borne in the lower leaf axils, containing 3-many clustered male flowers on pedicels 1.5–5 mm long; the cymes borne in the uppermost leaf axils contain 1-several bisexual flowers on pedicels 8–10 mm long, intermediate cymules consisting of both male and bisexual flowers; axis and pedicels usually densely tawny-pubescent.Sepals 4–5, 1.5–3 mm long, pubescent. Fruit a drupe, globose, 5-10 mm long, 4-6 mm wide, dark-purple, endocarp 6x6 mm, ovoid, polygonal, rough. Pollen grains triporate, oblate spheroidal.

Distribution: North Africa, Mediterranean area, Turkey to Afghanistan (map 7.3).
Habitat and ecology: Dry and upland areas (400-1500m).



Distribution map 7.3. *Celtis australis* in Africa.

Specimens examined:
***Celtis australis* L.**
ALGERIA: Chiffa Gorge (Blida -Medea), 11 June 1971, *Davis, P.H. 53446* (BM); Mustapha, April 1879, *Gandoger, A.M. 878* (C);
AZERBAIJAN: **Gyandzha**: "eastern Armenia", Elisabethopol [=Gyandzha], May, *Hohenacker, R.F. s.n.* (WAG);
CANARY ISLANDS (SPAIN): **Gran Canaria**: Tafiva (Vivsul), 29 November 1966, *Kunkel, G. 7721* (G); Bw. la Virgen, 11 May 1967, *Kunkel, G. 11080* (G); Gar. la Virgen, 11 May 1967, *Kunkel, G. 11081* (G);
FRANCE: **Gard**: Le Vigan, 22 April 1860, *Billot, P.C. 3202* (WAG); **Hérault**: St. Georges d'Orques, 7 April 1959, *Touw, A. 106* (WAG); **Pyrénées-Orientales**: near Argelès-s-Mer, July 1991, *Nek, F.I. van 851* (WAG; not seen!);
ITALY: **Palermo**: Palermo, ad vias, in dumetis reg. infer., in saxosis reg. montanae, 1 May 1900, *Ross, H. 67* (WAG); **Siena**: side of Mont Pisan near Asciano (Toscane), 16 March 1861, *Billot, P.C. 3202 bis* (WAG); **Süd Tirol**: Bozen, *Hausmann, F. von s.n.* (WAG); Merano, Tappeinerweg, 30 July 1929, *Ooststroom, S.J. van 2564* (L); between Schlanders [Silandro] and Meran, Vintschgau, July 1843, *Tappeiner s.n.* (WAG);
MOROCCO: **Fès-Boulemane**: Ouezzan, June 1909, *Gandoger, A.M. s.n.* (G, MO, NY); **Taza**: Middle Atlas of Morocco, 27 April 1969, *Søndergård, P. s.n.* (AAU, C); **Unknown**: Meknès, June 1982, *Casas, F. 7189* (G); GA. oued Moulay Brahim below Asni (above Marrakech), 14 April 1969, *Davis, P.H. 49362* (BM); Beni Hamed (Ktama), 30 January 1929, *Font Quer, P. 102* (BM); Ouirgane (Haut Atlas), 10 April 1979, *Lewalle, J. s.n.* (WAG); 1865, *Mandon, G. s.n.* (G); Asni, 9 April 1936, *Paulsen, O.W. s.n.* (C); Mountains near Idni, between Tizi-n-Test and Asni, 5 May 1961, *Wilde, J.J.F.E. de 2122* (BM, BR, WAG);

SOUTH AFRICA: **Transvaal**: Pretoria, Weavind Park, Christian Brothers College, Mount Edmund, 17 April 2002, *Heilgendorff, H. PRE 62793* (WAG); Pretoria, Sunnyside, Relly Street. (2528CA), 21 February 1981, *Toit, L. du 172* (WAG); **Unknown**: Cultivated. 2628AA, 23 January 1999, *Glen, H.F. 3898* (PRE);
SPAIN: **Granada**: Village Guejar-Sierra, 19 July 1996, *Jongkind, C.C.H. 2919* (WAG); **Murcia**: Sierra de Fuensanta near Murcia, 2 May 1850, *Bourgeau, E. Spain series 879* (WAG); **Unknown**: Pyrenees, Orgeganya, 23 June 1980, *Wijnands, D.O. 714* (WAG);
TUNISIA: Dorsale, Zoghauau, 3 May 1963, *Couteaux, G. 63T 13* (BR); May 1906, *Cuénod, A.J. s.n.* (G);
TURKEY: Adrianopel [=Edirne], *Noë, F.W. s.n.* (WAG).

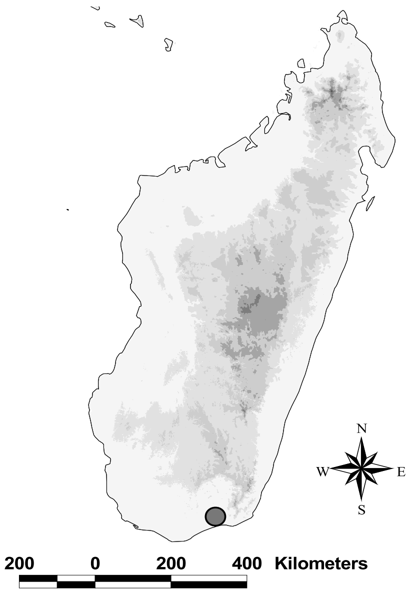
4. *Celtis bifida* J.-F. Leroy

Bull. Soc. Bot. France 95 (1948) 7. Type: Madagascar, Grève, 212 (holo: P).

Tree, 6-12 m tall, deciduous, monoecious, branchlets and young petioles rufescent (rusty)-pubescent tomentose, leaf blade entire, alternate, ovate or oblong-lanceolate, 4-7 cm long, 3-5 cm wide, below the tip subcrenate or wavy, the base obtuse or somewhat subemarginate, often slightly unequal, top gradually or suddenly becoming an obtuse acumen (tip), young ones pubescent-hirtellous, later glabrous, shiny, lateral veins 3-5, petiole 6-7 mm long, Axillary cymes with many flowers, male below, polygamous above, male flowers at the lower part, hermaphrodite flowers on top, usually longer than the petioles or slightly shorter. Male flowers subsessile or short-pedicellate; perigonium 5-parted, rarely 4-6-fid, lobes boat-shaped, slightly tomentose, margin slightly ciliolate (with hairs). Stamens 5-6, opposite the perianth lobes, inserted on a hairy disc, anthers 0.6-0.7 mm long, filaments 0.8-0.9 mm long. Rudimentary ovary small, top emarginated, disk strongly hispid. Hermaphrodite flowers: perigonium 5-fid, ovary elliptical or globose ± acuminate, pubescent, stigma linear, tip strongly bifid. Fruit a drupe subglabrous or thinly short-pubescent, ellipsoid or globose , 5-7 mm long, 3-5 mm wide, linear rather bifid, tip rather persistent, about 3 mm long, endocarp 6x5 mm ovoid, polygonal, rough. Pollen grains triporate, prolate, spheroidal.

Distribution: Endemic of Madagascar (map 7.4).
Habitat and ecology: In forests, especially along the margins.

Specimens examined:
MADAGASCAR: Central Madagascar, Berenty, April 1985, *O'Connor, S. 41* (K).



Distribution map 7.4. *Celtis bifida* in Madagascar.

5. ***Celtis gomphophylla*** Baker

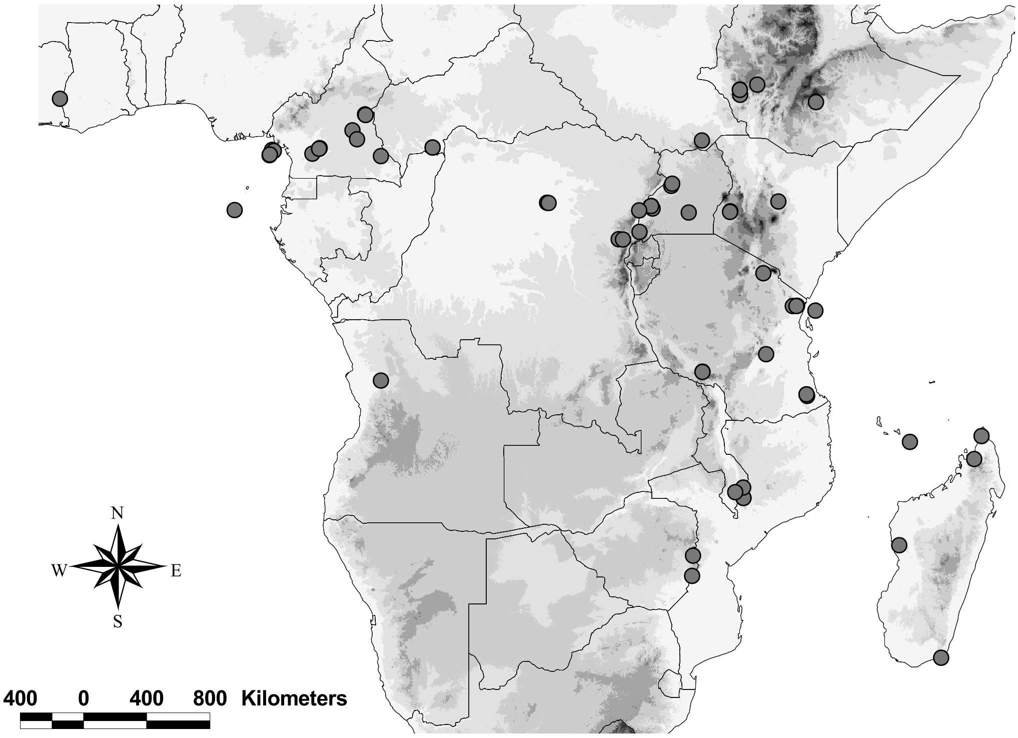
Bot. J. Linn. Soc. 22 (1887) 251; Leroy in Fl. Madag., fam. 54 (1952) 6. t. 3, fig. 5–8; Letouzey, Fl. Cameroun 8 (1968) 39, tabs. 2 fig. 4 & t. 5 figs. 1–2; K. Goates Palgrave, Trees Southern Africa (1977) 97 Tab. 3; Beentje, Kenya Trees, Shrubs & Lianas (1994) 318. Type: Madagascar, Central Madagascar, *Baron 3697* (holo: K; iso: BR, P)

Synonyms:
Celtis durandii Engl. Notizbl. Bot. Gart. Berlin 3 (1900) 22. Type: Tanganyika, Usagara, *Trotha 171* (B, syntype!) & Congo Republic, Bas-Congo, Dupuis (syn: B, isosyn: BR); *C. ugandensis* Rendle, Journ. Bot. 44 (1906) 341. Type: Uganda, Entebbe, Victoria Nyanza, *Bagshawe 669* (holo: BM); *C. dioica* S. Moore, Bot. J. Linn. Soc. 40 (1911) 204; type: Southern Rhodesia, Chirinda forest, *Swynnerton 108* (holotype: BM, isotype: K). *C. durandii* var. *ugandensis* (Rendle) Rendle, FTA 6, 2 (1916) 5.

Tree, 3–30 (-50) m tall, decidous, monoecious, bole often fluted or buttressed, bark smooth light grey, wood unpleasant smelling, young stems and branches whitish-pubescent, leaf blades entire, alternate, ovate-elliptic to oblong-elliptic, 6-16 cm long, 2-5 cm wide, apex long-acuminate; base cuneate to oblate, asymmetrical, (juvenile foliage up to 21x9 cm with apex long-acuminate (13 mm), lamina membranous-chartaceous, glabrescent, often scabrid, 3-nerved from the base with the basal lateral nerves not or hardly extending into the upper half, upper lateral nerves (2)3–6 on each side of the midrib, prominent above, more strongly so below, usually making an angle of less than 45 degrees with the midrib; Petiole 4–8 mm long. Stipules 2–6 mm long, linear to linear-oblong, whitish pubescent, caducous. Flowers precocious; male flowers in numerous, crowded, few-many-flowered. Cymes, pedicels 3–7 mm long, bisexual flowers few or solitary, pedicels often longer. Sepals 4–5, 1.2–2 mm long, pubescent, ovary ± pubescent or glabrous, styles unbranched, 2–2.5 mm long. Fruit a drupe, conical-ovoid, often 4-angled when dry often 4-7 mm long, 3-5 mm dark brown or black, endocarp 4x3 mm, angular-ovoid, polygonal, rough. Pollen grains triporate and prolate-spheroidal.

Distribution: Nigeria, São Tomé, Cameroon, Angola, Southern Africa, Madagascar (map 7.5).
Habitat and ecology: Low land and upland rain forest (500-1500m).

Specimens examined:
Celtis gomphophylla Baker
ANGOLA: Cuanza Norte: Cazengo, Granja de S. Luiz, *Gossweiler, J. 4536* (C, COI); **CAMEROON: Central Province**: 9 km from Yaoundé, road to Makak, path to Eloumden, 2 November 1961, *Breteler, F.J. 1996* (WAG); 9 km from Yaoundé, road to Makak, path to Eloumden, 2 October 1962, *Breteler, F.J. 3036* (WAG); 9 km from Yaoundé, road to Makak, path to Eloumden, 4 April 1962, *Bruijn, J. de s.n.* (WAG); near Nguna, 50 km ESE of Yaoundé, 21 June 1972, *Letouzey, R. 11341* (P); 40 km E of Mbalmayo, between Emamemuam and Kondesson, 23 June 1972, *Letouzey, R. 11345* (P); along road and side paths from road between Libamba and Kaya, c. 6 km E of Makak, 5 June 1987, *Manning, S.D. 1920* (MO, WAG); **East Province**: Road from Bétaré Oya to the North, edge of the Lom river near Monay, 28 February 1961, *Breteler, F.J. 1159* (BR, FI, K, LISC, M, P, WAG); NW of village Ndjangané, road to Ebaka, 47 km NW of Bertoua, 22 May 1961, *Breteler, F.J. 1396* (BR, K, LISC, M, P, WAG, YA); 15 km S of Yokadouma, road to Moloundou, 22 June 1961, *Breteler, F.J. 1551* (K, P, WAG, YA); NW of Kissi, 28 February 1961, *Letouzey, R. 3562* (G, P); Dimako (between Bertoua & Doume), 9 July 1963, *Letouzey, R. 5422* (BR, WAG); **South Province**: Bipindi, Lokundje-Thal, 1912, *Zenker, G.A. 4586* (G);
CENTRAL AFRICAN REPUBLIC: **Lobaye**: Oubangui, Boukoko, 4 April 1961, *Tisserant, C. 2055* (G, P); Oubangui. region Mbai'ki, Bokoko, 27 March 1949, *Tisserant, C., Equipe 1417* (WAG);
CONGO (KINSHASA): **Bas-Congo**: Thysville, Matete Forest ("INEAC Vuazi" [either locality or the herbarium? prob. not too far from institute], 21 March 1957, *Dubois, J. 180* (BR); **Nord-Kivu**: Nyange Bukombo, 8 April 1958, *Gutzwiller, R. 3628* (BR, WAG); Kitshanga, 9 January 1959, *Léonard, A. 2441* (BR, WAG); Beni-Kasindi road, near turning to Mutwanga, 21 September 1952, *Osmaston, H.A. 2648* (BM); **Orientale**: Yangambi, Island Esali, 14 April 1944, *Louis, J. 16984* (B, C); Yangambi, Island Tofuse, 27 August 1947, *Léonard, J.J.G. 1401* (B, C);



Distribution map 7.5. *Celtis gomphophylla* in Africa.

EQUATORIAL GUINEA: **Bioco (Fernando Poo)**: Malabo, cerca da povoaçao de Baney, 25 July 1986, *Carvalho, M.F. de 2096* (MA, WAG); Malabo-Rebola, km 5, 32NMK7914, 20 August 1986, *Carvalho, M.F. de 2358* (WAG); Malabo-Cupapa, km 2-3, 32NMK7714, 26 March 1989, *Carvalho, M.F. de 3848* (WAG); Bioco between Luba and Moeri, 13 July 1986, *Carvalho, M.F. de 10347* (MA, P); Bioco, Malabo-Rebola km 5, 1991, *Fernández Casas, F.J. 2358* (P); Between Luba and Moeri, near Bombe, 32NMJ6083, 13 July 1986, *Fernández Casas, F.J. 10347* (MA, WAG);
ETHIOPIA: **Illubabor**: Tepi, March 1977, *Chaffey, D.R. 1276* (K); 3 km S of Tepi, Along the road to Mezan Tefari, 11 December 1984, *Friis, I. 4139* (C, K); **Kaffa**: along road from Jimma to Bonga, 18 March 1976, *Jansen, P.C.M. 5304* (ACD, WAG); **Kefa**: 20 km SW of aman (Mezan Tefari airstrip), 29 November 1984, *Friis, I. 3864* (E); **Unknown**: 13 km N of Dolo Menna (Masslo), on the road to Goba, 25 October 1984, *Friis, I. 3484* (C, K);
IVORY COAST: **Abengourou**: Surroundings of Naiblé, 30 km E of Abengourou, 31 July 1969, *Versteegh, C. 616* (WAG);
KENYA: **Eastern**: Meru District, upper Imenti forest, 28 June 1974, *Faden, R.B. 74/ 908* (MO, WAG); **Nyanza**: Nyanza Province, North Kavirondo Distr, Kakamega Forest Station, 17 September 1949, *Maas Geesteranus, R.A. 6266* (WAG); **Western**: Kakamega Forest, near Forest Station, 11 April 1973, *Hansen, O.J. 900* (C);
MADAGASCAR: **Antsiranana (Diego Suarez)**: between Maivantana and Antanamarina, Ambanja, Antsiranana, 10 October 1998, *Antilahimena, P. 381* (MO, WAG); c. 35 km SW of Antsiranana, park National Montangne d'Ambre, near Joffreville, N of grand cascade, 17 February 1992, *Malcomber, S.T. 1257* (K, MO); **Toliara (Tulear)**: Toliara, [Andohahela RN], 29 January 1990, *Dumetz, N. 1276* (MO); **Unknown**: South central, Berenty, April 1985, *O'Connor, A.J. 20* (K);
MALAWI: **Northern Province**: Misuku Hills, Mugesse Forest, 1 October 1982, *Dowsett-Lemaire, F. Ecol 8* (BR, FHO); **Southern Province**: Foot of Mt. Mulanje, between Chitakale and Likhabula Forest Depot, 50 m from thr road, 19 December 1985, *Chapman, J.D. 6963* (MO); Mt. Mulanje foot, River Ruo bank at Wykesmith' s Grave, 26 October 1988, *Chapman, J.D. 9361* (E, MO); Phirilongwe Hill, 16 October 1983, *Dowsett-Lemaire, F. Ecol 259* (BR, FHO); **Unknown**: Lisau Saddle in Chiradzulu, 14 January 1982, *Chapman, J.D. 6091* (BR); Mingoli Estate, Zomba, Likangala, 17 June 1982, *Chapman, J.D. 6242* (BR);
MAYOTTE: Plage Sohoa, 16 October 1997, *Soumille, O. 985* (G, MO); 28 October 1997, *Soumille, O. 989* (G);
SAO TOMÉ AND PRINCIPE: **Sao Tomé Island**: Sao Tomé island, around Boa Entrada, nearby area, 1 August 1905, *Chevalier, A. 14479* (WAG);
SOUTH AFRICA: **Transvaal**: Johns on Umtata road, 19 March 1955, *Marais, W.R.B. 468* (FHO, MO; not seen!); **Unknown**: 27 km S of Lugwavuma, 5 March 1973, *White, F. 10431* (FHO, MO; not seen!);
SUDAN: **Eastern Equatoria**: Imatong mountains, Acholi Hills, Upper Talanga tea project area, November 1981, *Howard, W.J. UTT 17* (C);

TANZANIA: **Arusha**: Arusha District, Usa sawmills, logging track, one mile from hill, 30 March 1951, *Hughes, S.J. 67* (BR); **Kilimanjaro**: Morogoro, Kilombero District, Reserve above Sanje village, 26 August 1984, *Thomas, D.W. 3744* (MO); **Lindi**: Lindi Distr, Rondo Plateau, 20 February 1991, *Abdallah, R. 1679* (K, MO); Rondo Plateau, 7 February 1991, *Bidgood, S. 1381* (K, MO); Rondo plateau, Rondo Forest Reserve, 20 February 1991, *Bidgood, S. 1679* (C, K); **Mbeya**: Pungaluma Hills, about 1.2 km NE of Mshewe village, along the Mshewe River, 2 January 1998, *Gereau, R.E. 6119* (MO, WAG); Mbeya District, Mshewe, 31 November 1990, *Lovett, J.C. 4894* (MO, WAG); **Tanga**: between Amani and Kwamkoro, 2 August 1974, *Baagøe, J. 200* (C, WAG); Korogwe District, (T3) old Ambangulu Village, N of Msambiyazi and Kwemasimba villages, 25 January 1999, *Mwangoka, M.A. 242* (MO); Monga, 18 August 1986, *Ruffo, C.K. 1763* (C, K); **Unknown**: Amani, March 1903, *Warnecke, O. 350* (E, P);
UGANDA: **Central Province**: Mabira forest, October 1908, *Ussher, C.B. 65* (BM); **Unknown**: Kajansi, October 1937, *Chandler, P. 2047* (P); Kipayo, 15 January 1914, *Dümmer, R.A. 584* (BM, P); Masindi Distict, Budongo forest, Kaniyo-Pabidi, *Hafashimana, D.L.N. 48* (E); Kabarole district, Kibale, Forest; Nagogo, June 1997, *Hafashimana, D.L.N. 177* (E); District: Kabarole, Burahya County. Kibale National Park. Near Kanyawara, 15 October 1995, *Nkuutu, D.N. 8*- 86 (C); **Western Province**: Budongo Forest Reserve, Nature Reserve, close to the Sonso River, 25 August 1995, *Nkuutu, D.N. 7- 52* (C); District Rukungiri, Bwindi National Park, Northern Sector (Kayonza), on slopes near the Ishasha River, 23 February 1995, *Nkuutu, D.N. 5- 72* (C);
ZIMBABWE: **Chipinga**: Chirinda Forest, October 1965, *Goldsmith, B. 65/ 26* (BR); **Manicaland**: Umatali District, *Corner, S.G. s.n.* (E).

6. ***Celtis malagasica*** Sattarian *nom. nov.*

Based on *C. madagascariensis* Sattarian *nom. inval.*, Blumea 50 (2005) 501. Type: Madagascar: Toliara, Reserve d’Andohalela, parcelle 2, near Hazofotsy, along river bank: *Phillipson 2938*, 20 Dec. 1988, fl. (holo: MO; iso: WAG).

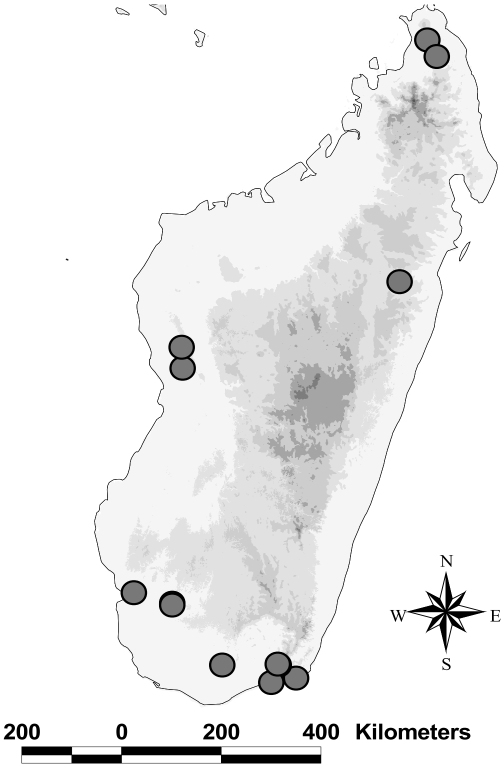
Small tree, 7 - 10 m high, bark grey, whitish, smooth. Leaves alternate, simple, ovate-elliptic, 7 - 10 x 2.5 - 3 cm, coriaceous, petiole 7 - 14 mm long, margin entire, attenuate or rounded at base, 3 veins at base, midrib reaching the apex, two lateral veins reaching 2/3 of leaf length, running close to the margin at ¼ or less of the distance from midrib to margin, no conspicuous additional lateral veins, leaf apex obtuse-mucronate. Inflorescences axillary, as long as or clearly longer than the petiole, lower ones with male flowers only or with male flowers and 1--2 hermaphrodite flowers, upper ones sometimes without male flowers and 2 - 5 hermaphrodite flowers. Male and hermaphrodite flowers creamy with a tender glabrous pedicel, 3 - 5 mm long. Sepals 5, glabrous; stamens 5, filaments shaped as an acumen, often bent during flowering, 5-9 mm long, anthers 1 mm long, ovate-globose. Fruit a drupe, broadly ellipsoid, c. 12 x 8 mm, 1-seeded, green becoming red or brown, endocarp ovoid-acuminate, polygonal, surface reticulate, creamy-whitish.

Distribution: Endemic of Madagascar. (map 7.6).
Habitat and ecology: in the margin of the forest, lowland.

Note: Because an older version of the electronic database (Int. Plant Names Index) was consulted, the name *Celtis madagascariensis* Boj., Hort. Maurit. 296 (1837) was overlooked. This name is a nomen semi-nudum, and a synonym of *Trema orientalis* L. (Index Kewensis 1895). It appeared the most prudent to select a new name for the species.

Specimens examined:
Celtis malagasica Sattarian
MADAGASCAR: **Antsiranana (Diego Suarez)**: sous-préfecture de Vohemar, commune rurale de Dariana. Forêt de Bekaraoka, partie sud, Andranotsimaty. Aux abords du village d' Andranotsimaty, 7 November 2001, *Gautier, L. 4094* (G, WAG); Antsiranana (Diego Suarez) region, Ankarana RS, S of town, 24 November 1989, *McPherson, G. 14535* (MO); **Mahajanga (Majunga)**: Tsingy de Bemaraha north of the Manambolo river, 10 December 1996, *Jongkind, C.C.H. 3477* (WAG); Reserve Naturelle de Bemeraha SE of Antsalova, 23 August 1987, *Phillipson, P.B. 2254* (WAG); **Toamasina (Tamatave)**: 1.5 km SE of Ankosy, outside near of national park of Zahamena, 25 January 2000, *Rakotondrajaona, R. 117* (MO); **Toliara (Tulear)**: Fort Dauphin (Tolanaro) region, SW of town in forest called

Petriky, along QIT road, 12 January 1990, *McPherson, G. 14772* (MO, WAG); Beza Mahafaly RS, near Ambinda, 3 November 1987, *Phillipson, P.B. 2509* (MO); Beza Mahafaly RS, Beza Betioky. Ehazoara River valley E of Sakamena River, 15 November 1987, *Phillipson, P.B. 2565* (MO, WAG); Reserve d' Andohalela, parcelle 2, near Hazofosty, along river banks, 20 December 1988, *Phillipson, P.B. 2938* (MO, WAG); Toliara, Integral Natural Reserve of Andohahela. Parcelle No. 2, 18 March 1994, *Rahajasoa, G. 226* (MO); Andohahela Reserve intergrale 11, zone no 2, Inhazofosty, 2 March 1993, *Randriamampionona, B. 147* (MO); 16 km SE of the crossing with national road 7, banks of the River Onilahy, 9 February 2000, *Randrianaivo, R. 496* (MO); Dunes of Mandrare, 22 September 1950, *Service Forestier de Madagascar SF 1558* (TAN); 40 km NE of Betioky, near Analafaly, *Sussman, L. 436 A* (MO).

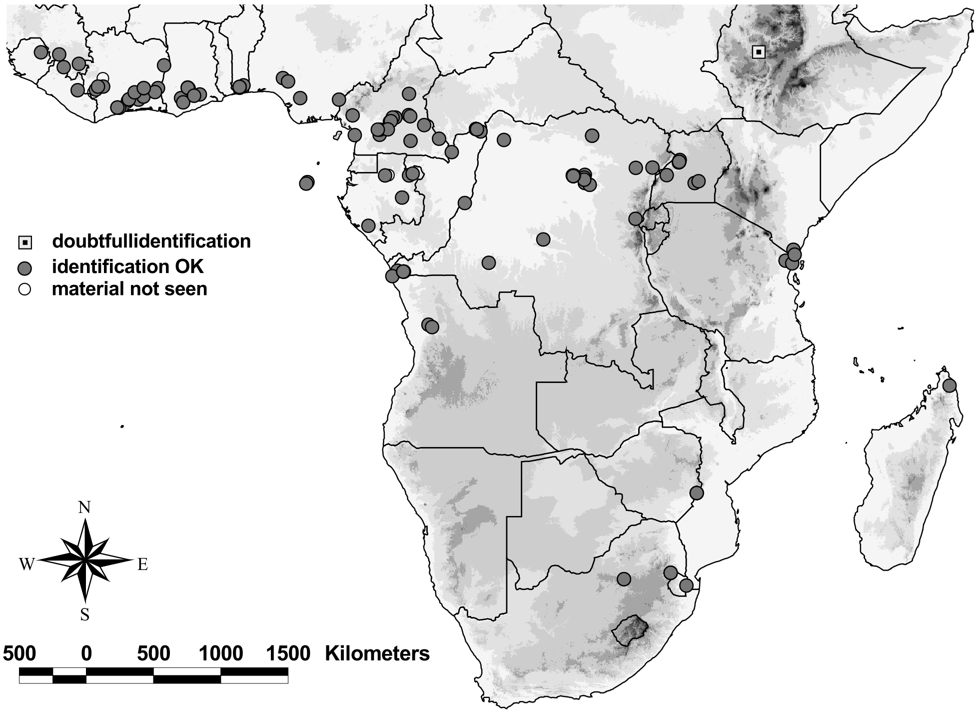


Distribution map 7.6. *Celtis malagasica* in Madagascar.

7. ***Celtis mildbraedii*** Engl.

Bot. Jahrb. Syst. 43 (1909) 309; in Mildbr. Wiss. Ergebn. Deutsch. Zentral-Afr.-Exped. 1907–1908, 2 (1911) 180, t. 16, fig. E; Pflanzenw. Afr. (1915) 14; Hauman in Fl. Congo-belge 1(1948) 45; Keay in Fl. W. Trop. Afr. ed. 2, 1(1958) 592; Polhill in Kew Bull.19 (1964) 140; in F.T.E.A., Ulmaceae: 7 (1966); Letouzey in Fl. Cameroun 8 (1968) 33, tabs. 3, 4 fig. 2 & t. 5 fig. 4; Palmer & Pitman, Trees of S. Afr.1 (1972) 427, t. & photo; K. Coates Palgrave, Trees Southern Africa (1977) 97. Beentje, Kenya Trees, Shrubs & Lianas (1994) 318. Type: Congo Republic, Orientale, *Mildbread 2897* (lectotype B, photo: K).

Synonyms:
Celtis usambarensis Engl., Bot. Jahrb. Syst. 43 (1909) 309. Type: Tanganyika, East Usambara, *Zimmermann in herb. Amani 853* (holo: B); *C. compressa A. Chev*., Bull. Soc. Bot. France 61, mém. 8 (1917) 298. Type: Ivory Coast, Bouroukrou, railroad km 92, 20 Dec. 1906 - 20 Jan. 1907, *Chevalier 22451, 22460* (holo: P, isolectotype: BR); *C. dubia* De Wild., Rev. Zool. Afr. 9, suppl. Bot. 5 (1921), & Pl. Bequaert. (1922) 190. Type: Congo Republic, *Bequaert 2525* (holotype: BR); *C. franksiae* .N.E. Brown., Fl. Cap. 5 (2) (1920) 517. Type: South Africa, *Franks in herb. M. Wood 11726* (holo: K).



Distribution map 7.7. *Celtis mildbraedii* in Africa.

Tree, 10–40 m tall, evergreen or deciduous, monoecious, branches often drooping, trunk with buttresses, bark pale smooth or scaling in small disks.Young twigs tawny-pubescent, leaf margin obscurely crenate to coarsely dentate in the upper half, alternate, elliptic to elliptic-obovate, 9–15 cm long, 4–6 cm wide, apex long acuminate if tree is juvenile, otherwise ± mucronate, base cuneate, slightly asymmetrical, lamina chartaceous to thinly coriaceous, venation basal lateral veins longer than the middle of the leaf; very young leaves sparsely tawny-pubescent; petiole 3–7 mm long. Stipules 4–5 mm long, lanceolate, tawny-pubescent. Cymes 4–15 mm long, of many, rarely few, often crowded male flowers with pedicels up to 2 mm long, bisexual flowers 1 or few at the apex of the cyme, uppermost cymules of the inflorescence with several bisexual flowers.Sepals 5-6, 1.5–2 mm long, pubescent. Ovary often with a ring of sparse hairs at the base, otherwise subglabrous, styles branched once or twice. Fruits a drupe, ovoid-ellipsoid, 4-ribbed when dry, 7-10 mm long, 5-6 mm wide, red or black, endocarp 6x5 mm, rhomboid, polygonal, rough. Pollen grains triporate and prolate spheroidal.

Distribution: Sudan, Congo to West Africa (map 7.7).
Habitat and ecology: lowland forest and margins of forest (200-800 m).

Note: Two of the four syntypes of *Celtis soyauxii* Engl. belong to *C. mildbraedii*, and this name has been misapplied in the past for *C. mildbraedii*, see note under *C. zenkeri*.

Specimens examined:
***Celtis milbraedii* Engl.**

ANGOLA: **Cuanza Norte**: District de Cazengo, 1903, *Gossweiler, J. 613* (P, WAG); **Unknown**: Golungo-Alto, *Welwitsch, F.M.J. 6298* (BM);

BENIN: **Atacora**: forêt classée de Pénéssoulou, 30 August 1988, *Houngnon, P. 4607* (BENIN); **Atlantique**: Niaouli, 5 October 1999, *Akoègninou, A. 2981* (BENIN, WAG); Niaouli, 29 May 2000, *Akoègninou, A. 3327* (BENIN); Dahomey: Cercle d'Allada, Niaouli, près Allada, 29 March 1910, *Chevalier, A. 23407* (P, WAG); Niaouli, 9 September 1998, *Essou, J.-P. 1138* (BENIN, WAG); Niaouli, 23 August 1999, *Essou, J.-P. 1648* (BENIN, WAG); Forêt de Djigbé, 7

November 1997, *Ganglo, J. 15* (BENIN, BRLU, WAG); Niaouli, 11 May 1988, *Houngnon, P. 4392* (BENIN); **Ouémé**: Pobè, 12 November 1988, *Sokpon, N. B 13* (BRLU; not seen!);

CAMEROON: **Central Province**: Vimeli (=Mbalmayo), 1928, *Hédin, L. 1661* (P, WAG); Essam, 13 February 1959, *Letouzey, R. 1238* (P); Kouambang I (IGN sheet Nanga-Eboko), 11 April 1959, *Letouzey, R. 1594* (P, WAG); Membine, 9 May 1959, *Letouzey, R. 1894* (P); Membine, 9 May 1959, *Letouzey, R. 1895* (P); 25 km WNW of Akonolinga, Mengang, 9 March 1962, *Letouzey, R. 4517* (P); near Yaoundé, near Nkolbison (about 1 hour over the road W of Yaoundé), Marécage, 11 March 1981, *Meijer, W. 15029 B* (MO); near Yaoundé, 1956, *Rerolle, P. 5* (P); **East Province**: 10 km N of Ndemba II = 30 km N of km 29 of road Bertoua-Nanga Eboko, 16 June 1965, *Leeuwenberg, A.J.M. 5915* (BR, P, WAG, YA); Gere, map sheet IGN, 1/200.000 Yoko, 29 June 1959, *Letouzey, R. 2297* (P, WAG); SW of Lomie, map sheet IGN 1/200.000 Abong-Mbang, 31 March 1961, *Letouzey, R. 3655* (P, WAG); Batanga, 30 km SSE of Batouri, 7 April 1964, *Letouzey, R. 4693* (P); 25 km S of Moboy, (45 km East of Yokadouma), Map IGN 1/200.000 Yokadouma, 15 May 1963, *Letouzey, R. 5052* (P, WAG); **Littoral Province**: Subdivision Bassa, 25 km Douala, road Razel, 12 May 1956, *Endengle, E. 37* (P); **North Province**: 12 km SW of Dir, in the bend of Baoko river (IGN sheet Bagodo), 31 July 1966, *Letouzey, R. 7585* (P);

CENTRAL AFRICAN REPUBLIC: **Lobaye**: N side of road N' Baïki-Zinga in the S.E.F.I. permit, 4 December 1955, *Tellier E-222- 2* (P); Boukoko. Oubangui-Chari, 28 October 1951, *Tisserant, C. 1130* (P, WAG); Oubangui: Région de Mbaïki & Boukoko, 17 July 1951, *Tisserant, C. 2174* (P, WAG); Station of Bukoko, 24 November 1947, *Tisserant, C., Equipe 486* (P); 6 September 1948, *Tisserant, C., Equipe 1130* (P); between Mbaiki and Boukoko, 17 January 1951, *Tisserant, C., Equipe 2174* (P); Station of Boukoko, 23 March 1953, *Tisserant, C., Equipe 2485* (BM, P); **Unknown**: Nadakan, upland forest 3 km E of Sango River, 11 May 1988, *Gentry, A.H. 62710* (MO); Region of Mbaiki and Boukoko, 23 November 1950, *Tisserant, C. 1943* (BR);

CONGO (BRAZZAVILLE): Sembé, Forêt de Bellevue, 15 June 1972, *Sita, P. 3374* (WAG);

CONGO (KINSHASA): **Bandundu**: 7 November 1990, *Masens, B. 210* (BR, WAG); **Bas-Congo**: Station INERA of Luki, 26 November 1983, *Breyne, H. 4680* (BR); road to Tshoa, 21 September 1945, *Donis, C. 1380* (BR, C); Kiobo, 2 October 1957, *Matton, J. 29* (BR); Luki, Parc de la N'kula, 29 October 1948, *Maudoux, E. 95* (BR, WAG); N'kula valley, 23 January 1948, *Toussaint, L. 171* (BR, P); Moanda, between Tondé River and the Mission, behind the house of Brouhns, at fork in road to Moanda, 25 April 1954, *Wagemans, J. 794* (BR); INEAC- Luki, within village of Kinkoko, 7 March 1959, *Wagemans, J. 2104* (BR); Ineac-Luki, 7 February 1959, *Wagemans, J. 2116* (BR); **Equateur**: Lukolela, 23 March 1931, *Chapin, J.P. 662* (BM); Station INÉAC Boketa, 28 July 1955, *Evrard, C. 1459* (BR); **Kasai Oriental**: Prov: Kasai, Kole on Lukenie, 3 May 1955, *Cauwe, G. 3053* (BM, BR, C); **Orientale**: 30 km along road from Kisangani to Bengamisa, 6 June 1973, *Bokdam, J. 4164* (KIS, WAG); 16 km along road from Kisangani to Bengamisa, 22 October 1973, *Bokdam, J. 4293* (WAG); Yangambi, 29 November 1951, *Donis, C. 3197* (MO); village of Ahungba (Irumu), July 1949, *Germain, R. 5282* (BR); Yangambi, 1947, *Gilbert, G. 7827* (BR); Yangambi, 1947, *Gilbert, G. 7960* (BR); Yangambi, 1947, *Gilbert, G. 8004* (BR); Yangambi , *Gilbert, G. 9155* (BR); Yangambi, 1948, *Gilbert, G. 9242* (BR); Harvested on the observation tree no 0-1960 in 1947 in Yangambi, 1947, *Gilbert, G. 10141* (BR, WAG); Bambesa, 5 September 1951, *Gérard, P. 21* (BR); Bambesa, 11 September 1951, *Gérard, P. 47* (BR, NY); Mambasa, (Ituri Forest) Lenda, 9 December 1992, *Hart, T.B. 1426* (K); 35 km of Kisangani- (raod of Wanie-Rukula), 29 June 1979, *Lisowski, S. 52653* (BR, K); 6 km NE of Yangambi, 25 February 1936, *Louis, J. 1362* (BR); Yangambi, 7 km NW of river, 12 May 1937, *Louis, J. 3849* (BR); Yangambi, valley of Mbutu, 29 November 1937, *Louis, J. 6806* (BR, FI); Yangambi, 23 July 1938, *Louis, J. 10471* (BR); Yangambi, Mbutu valley, 5 October 1938, *Louis, J. 11549* (BR, MO, NY); Yangambi, October 1941, *Louis, J. 16505* (BR, C); Yangambi, 6 November 1941, *Louis, J. 16507* (BM, BR); Wanie-Rukula, ile Kipokoso, 29 September 1978, *Mandango 2696* (BR); Yangambi, 3 March 1953, *Maudoux, E. 577* (BR); Yangambi, 19 June 1953, *Maudoux, E. 620* (BR); First transect Stanleyville 25 km, 5 April 1939, *Meiren, J.J. van der 89* (BR, C); **Sud-Kivu**: km 69 road Kavumu-Walikale, Bunyakiri, 3 September 1955, *Pierlot, R. 815* (BR);

ETHIOPIA: **Wollega**: c. 45 km from Nekemti, along road from Addis Ababa to Nekemti, 15 May 1976, *Jansen, P.C.M. 6244* (ACD, WAG);

GABON: **Nyanga**: Réserve de Monts Doudou, au Sud-Ouest de la Brigade de Moukalaba à Morindi, 20 March 2000, *Sosef, M.S.M. 874* (LBV, WAG); **Ogooué-Ivindo**: 12 950 m, Chantier SHM, Layon 'Z, 22 February 1988, *Dibata, J.J. 435* (LBV; not seen!); Boka-Boka, 4 March 1979, *Florence, J. 1703* (P); Batouala, between Makokou and Mekambo, 27 February 1961, *Hallé, N. 1361* (P, WAG); **Ogooué-Lolo**: about 30 km E of Lastoursville, 30 November 1991, *Breteler, F.J. 10844* (WAG); **Woleu-Ntem**: 33 km E de Mitzic, 13 April 1988, *Wilks, C.M. 1708* (LBV, WAG);

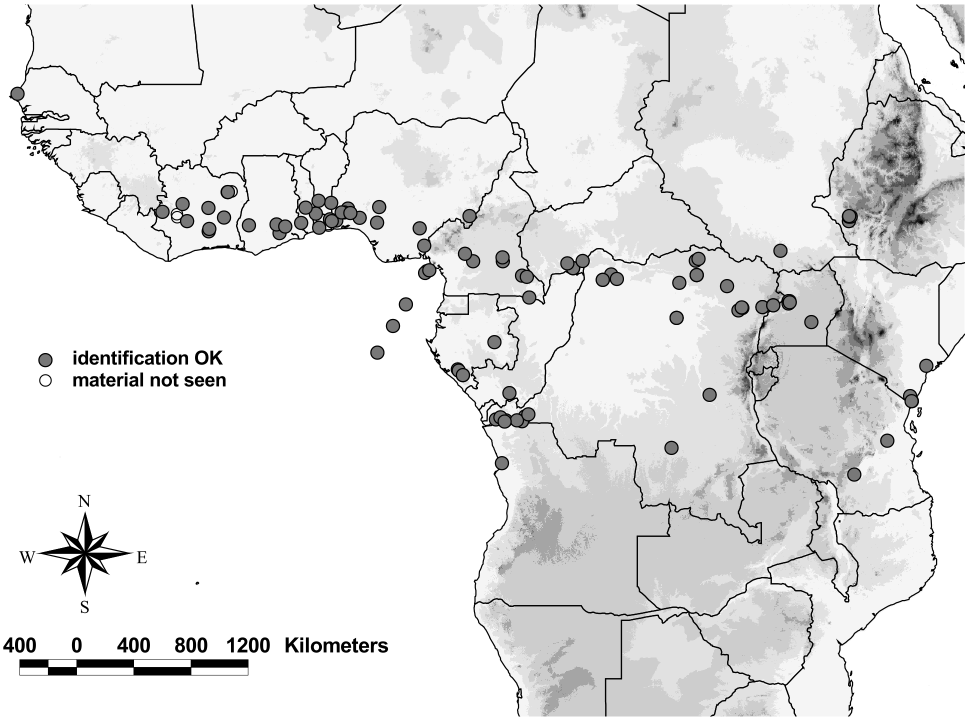
GHANA: **Ashanti Region**: Ashanti, Sekyere. Bobiri forest reserve, 20 September 1988, *Kisseadoo, S. 4* (US); Ashanti, Sekyere, Bobiri forest reserve, 25 September 1988, *Kisseadoo, S. 174* (MO); Ashanti Region: Bobiri F.R., E of Kumasi, NE of Kubeasi, 27 February 1979, *Leeuwenberg, A.J.M. 11977* (GC, WAG); **Eastern Region**: Kade A.R.S., 22 March 1970, *Enti, A.A. 40116* (P, US); Kade Agricultural Research Station, 1 April 1977, *Hall, J.B. GC 46572* (WAG); **Unknown**: Foso, 20 March 1973, *Enti, A.A.R 1185* (NY); Asiakwa District, Sagyimase village, c. 4 km NW of intersection of Accra-Kumasi road, 2 July 1995, *Harder, D.K. 3311* (MO); Dunkwa, February 1927, *Vigne, C. 257* (K, P);

GUINEA: **Kissidougou**: Bongoro, 14 April 1949, *Adam, J.G. 4419* (WAG); **Nzérékoré**: in village of Sibamou, 25 June 1949, *Adam, J.G. 5414* (MO);

IVORY COAST: **Abengourou**: 25 km east of Abengourou, along the road to Niablé, 31 July 1969, *Versteegh, C. 613* (WAG); **Adzopé**: on border of Comoé River, c.15 km NW of Mbasso; c.60 km NE of Adzopé, 27 July 1963, *Wilde, W.J.J.O. de 597* (WAG); **Agboville**: Bouroukrou, 9 January 1907, *Chevalier, A. 16926* (P); Bouroukrou, chemin de fer km 92, 5 January 1907, *Chevalier, A. 16932* (P, WAG); km 95 new road Abidjan-Ndouci, 1 October 1979, *Kruif, A.P.M. de 390* (UCJ, WAG); **Bondoukou**: 92 km of Chenive, January 1913, *Chevalier, A. 16152* (P); **Bongouanou**: Morénou, Bangouanou, 25 November 1909, *Chevalier, A. 22451* (P); **Divo**: Forêt de l'IRCC de Divo, 17 October 1990, *Chatelain, C. 322* (CSRS; not seen!); Forêt de l'IRCC de Divo, 17 October 1990, *Chatelain, C. 325* (CSRS; not seen!); NW forêt de la Boubo. Ouest du Village V3 de palme-industrie, 11 December 1990, *Chatelain, C. 587* (G; not seen!); 4 km W of Divo, 13 December 1990, *Chatelain, C. 596* (G; not seen!); Surroundings of IFCC, 10 km SE of Divo, 7 July 1969, *Versteegh, C. 411* (WAG); **Duékoué**: Between Issia and Duékoué, 20 February 1976, *Koning, J. de 6563* (WAG); **Guiglo**: 23 January 1957, *Aubréville, A. (Ivory Coast series) 13* (P, WAG); **Sassandra**: 64 km N of Sassandra, 3 km N of Niapidou, 29 January 1959, *Leeuwenberg, A.J.M. 2628* (WAG); 64 km N of Sassandra, 3 km N of Niapidou, 12 February 1959, *Leeuwenberg, A.J.M. 2723* (WAG); 72 km N of Sassandra, direction Lakota, 1 May 1962, *Leeuwenberg, A.J.M. 4078* (B, BR, EA, FHI, HBG, K, L, MO, NLI, P, PRE, SL, WAG); **Toumodi**: Orumbo Boka, 3 October 1956, *Wilde, J.J.F.E. de 629* (WAG); **Unknown**: Douékoue, 6 October 1949, *Adam, J.G. 6377* (MO); F.C. de Goin-Débé, centre, forêt peu dégradée (7km à l'intérieur de la FC.), 20 July 1996, *Chatelain, C. 1352* (CSRS; not seen!); September 1906, *Chevalier, A. 14346* (P); Dahomey, 2 January 1970, *Letouzey, R. 23407* (P); **Vavoua**: F.C. du Haut-Sassandra, Nord. entre layon 1 et limite Nord, 9 November 1993, *Kouamé, F.N. 728* (CSRS; not seen!);
KENYA: **Coast**: Kwale District, Mrima hill, 5 March 1977, *Faden, R.B. 77/ 678* (K, WAG); **Unknown**: near Maereni village, 24 April 1981, *Hawthorne, W.D. 414* (K);
LIBERIA: **Lofa**: Loma National Forest, 15 December 1961, *Voorhoeve, A.G. 739* (WAG); **Nimba**: Gio National Forest, Southern part, E slopes of the mountain ridge, 11 May 1961, *Voorhoeve, A.G. 287* (WAG);
MADAGASCAR: **Antsiranana (Diego Suarez)**: Région de Dariana. Sous-préfecture de Vohemar, commune rurale de Dariana, Forêt de Binara, camp I. 1.6 km WSW of camp, 9 November 2001, *Gautier, L. 4132* (G, WAG);
NIGERIA: **Cross River State**: Cross River North Forest Reserve. Compt. 1, Compt. 2. about 15 km SE of Ikom, 20 May 1971, *Meer, P.P.C. van 1724* (WAG); **Edo State**: Ubiaruku, Usonigbe Forest Reserve. BC 33/1, 21 August 1959, *Oladoyinbo, A. FHI 43361* (WAG); **Ondo State**: Province, Ondo, Division: Akure Locality Idanre, 5 January 1948, *Brenan, J.P.M. 5* (K); Province, Ondo, Locality, Akure, 20 August 1946, *Jones, A.P.D. 20703* (FHI, K, P); **Unknown**: *Kennedy, J.D. 1956* (BM); *Kennedy, J.D. 2400* (P);
SAO TOMÉ AND PRINCIPE: **Sao Tomé Island**: Sao Thomé, September 1905, *Chevalier, A. 1334* (P); San Thomé, Boa Entrada et environs, 1905, *Chevalier, A. 14345* (P, WAG);
SIERRA LEONE: **Northern Province**: Perankoro, 11 February 1966, *Adam, J.G. 23671* (MO);
SOUTH AFRICA: **Kwazulu-Natal**: Durban, Natal, 12 December 1910, *Franks, M. 11726* (E); Durban, Stella Bush, 27 May 1950, *Hilliard, O.M. 689* (E); **Natal**: Prov, Natal Dist, Durban, 5 November 1955, *Bayer, J. 1* (BM, PRE); Pigeon valley, Stella Bush, 12 December 1910, *Franks, M. 12813* (CO, PRE); Durban, Natal, 27 May 1950, *Hilliard, O.M. 686* (E);
SWAZILAND: **Unknown**: 28 km SE of Siteki, Jilobi forest, 9 October 1977, *Kemp, E.S. 996* (MO, WAG)
TANZANIA: **Tanga**: 3 km along road at Zigi Nursery, Amani Botanical Garden, Nimri camp, Kwamshinde, 18 November 1997, *Rajabu Hizza, I. 59* (MO); Lutindi Forest Reserve, 15 August 1986, *Ruffo, C.K. 1755* (K, WAG);
UGANDA: **U4 (Buganda flora region)**: 14 November 1962, *Styles, B.T. 207* (BRLU, ENT, K); **Unknown**: c. 1 mile W of Najembe H.Q on clearing of new Kampala-Jinja road, in Lwankima forest, immediately south of the Mabira. Hillside site on red-brown heavy loam, 14 April 1950, *Dawkins, H.C. D 599* (K); Masinidi District, Budongo forest, Kaniyo pabidi beat, February 1996, *Hafashimana, D.L.N. 33* (C); Kibale, 16 December 1938, *Loveridge, M.V. 252* (K); **Western Province**: Masindi District, Budongo forest Reserve, Nyakafunji Block, c. 2.5 km N of Nyabyeya Forest college, 15 June 1998, *African tropical Biodiversity Program 435* (MO); Budongo forest Reserve, Nyakafunjo Block, c. 3 km N of Nyabyeya Forest college at Sonso river, 18 July 1998, *African tropical Biodiversity Program 564* (MO); Budongo Forest Reserve, 25 August 1995, *Nkuutu, D.N. 6- 118* (C); Bundongo, 25 September 1962, *Styles, B.T. 75* (K);
ZIMBABWE: **Chipinga**: Chirinda Forest, February 1962, *Goldsmith, B. 62/ 56* (BR, K); Chirinda Forest, September 1962, *Goldsmith, B. 62/ 195* (K, MO, WAG); Chirinde forest interior, November 1962, *Goldsmith, B. 62/ 197* (BM, CAH); **Unknown**: Chirinda Forest, December 1962, *Goldsmith, B. 62/ 231* (MO, PRE); November 1997, *Wyk, P. van BSA 3351* (PER, PRE).

8. *Celtis prantlii* Priemer ex Engl.

Bot. Gart. Mus. Berl. 3 (1900) 23; in Mildbr. Wiss. Ergebn. Deutsch. Zentral-Afr.-Exped. 1907–1908, 2 (1911) 179; Engl., Pflanzenw. Afr. (1915) 12; Rendle in Fl. Trop. Afr. 6, 2(1916) 8; Hutch., Dalziel & Moss in Fl. W. Trop. Afr. 1(1928) 423; Hauman in Fl. Congo-belge 1(1948) 43; Robyns, Fl. Sperm. Parc Nat. Alb. 1 (1948) 44. Type: S. Tome, *Quintas 144* (B, lecotype).



Distribution map 7.8. *Celtis prantlii* in Africa.

Synonyms:
Celtis brownii Rendle, Journ. Bot. 53 (1915) 298; in Fl. Trop. Afr. 6, 2 (1916) 10; Keay in Fl. W. Trop. Afr. ed. 2, 1(1958) 592. Type: Uganda, Mabira Forest, *E. Brown 462* (lectotype: BM); *C. scotellioides* A. Chev., Bull. Soc. Bot. Fr. 61, Mém. 8e (1917) 299. Type: Ivory Coast, Haute-Sassandra, between Droupleu and Zoanlé, 5 May 1909, *Chevalier 21459* (holo: P (not seen); isotype: K!); *C. crenata* A. Chev., Expl. Bot. Afr. Occ. Franc. 1 (1920) 588. Type: Ivory Coast: Morénou, between Yaboisso and Daoukrou, 4 Dec. 1909, *Chevalier 22488* (syntype: P (not seen) & Benin: near Zagnanado, between Abbo and Massé, 6 Feb. 1910, *Chevalier 22575*, (syntype: P (not seen); iso: BR !); *C. rendleana* G. Tayl. in Exell, Cat. Vasc. Pl. S. Tomé: 302 (1944). Type: from Angola, *Welwitsch 6302* (holo: BM!; iso: K!).

Tree, 5–15m tall, deciduous, monoecious, trunk with short buttresses, bark smooth grey, wood white.Young twigs very sparsely white-pubescent, glabrescent, leaf blades dentate in upper half, alternate, elliptic to elliptic-ovate or elliptic-oblong, 6–10 cm long, 3–6 cm wide, apex with a wide acumen and mucronate tip, base slightly asymmetrical and broadly cuneate to rounded or subcordate; petiole 8 mm long, lamina thinly coriaceous, pale green, punctate but smooth and ± shiny above, glabrous, 3-nerved from the base, the basal lateral nerves extending almost to the apex, as strongly prominent beneath as the midrib, upper lateral nerves 1–2 (3) on each side of the midrib, rather fine and inconspicuous; secondary venation fairly closely parallel, ± horizontal between the midrib and basal lateral nerves. Petiole 4–10 mm long. Stipules 3–7 mm long, lanceolate, shortly produced below the point of attachment, ± pubescent. Inflorescences in leaf axils towards the ends of branches, lower inflorescences 5–30 mm long, containing many crowded male (lower ones, these sessile or with pedicels to 2 mm long, and a few female and bisexual flowers at apices of branches of these inflorescences, their pedicels usually longer; upper inflorescences usually short with several bisexual flowers, sepals 2–4 mm long, pubescent, ovary ± glabrous, with a basal ring of long hairs, styles very shortly bifid, 1.5–3 mm long. Fruit a drupe, ovoid, glabrous, 9–12 mm long, 7–10 mm wide, red to black, pedicels 3–7 mm long, endocarp 8x 6 mm, smooth, ovoid, polygonal, smooth. Pollen grains triporate, oblate spheroidal.

Distribution: Africa from west to east (map 7.8).
Habitat and ecology: low land and margin of forest (200-700 m).

Specimens examined:
Celtis prantlii Priemer ex Engl**.**

ANGOLA: **Unknown**: 24 September 1912, *Gossweiler, J. 5508* (BM);

BENIN: **Atlantique**: Reserve Forest of Ahozon few km N of RNIE 1, 3 February 2003, *Maesen, L.J.G. van der 7819* (BENIN, WAG); **Mono**: Kpédjihoudéhoué, 6 August 1998, *Essou, J.-P. 871* (BENIN, WAG); Kpédjihoundéhoué, 17 February 1999, *Essou, J.-P. 1439* (BENIN; not seen!); Ouèdèmè-Péda, 22 February 1999, *Essou, J.-P. 1549* (BENIN, WAG); **Ouémé**: Kogbédjo, 8 August 2001, *Adjakidjè, V. 4724* (BENIN, WAG); forêt de Ké, 26 May 2000, *Akoègninou, A. 3315* (BENIN; not seen!); Forêt de Toffo, 4-5 km W of Pobè, road to Adja-Ouèrè, 24 November 1998, *Maesen, L.J.G. van der 6635* (BENIN, WAG); **Unknown:** *Aubréville, A. 1439* (WAG); **Zou**: Oké Owo, 15 December 1999, *Adjakidjè, V. 3188* (BENIN, WAG); Lama, 20 June 1998, *Akoègninou, A. 1457* (BENIN; not seen!); Lougba, 21 July 1998, *Akoègninou, A. 1611* (BENIN, WAG); Lama, 21 January 1999, *Akoègninou, A. 1973* (BENIN; not seen!); forêt de Lama; layon 14; secteur de Koto; noyau central, 23 October 2001, *Essou, J.-P. 3187* (BENIN; not seen!); Malomi, on offroad to the west of RNIE 3 Savalou-Bantè, 21 September 2005, *Maesen, L.J.G. van der 8315* (BENIN, WAG);

CAMEROON: **Central Province**: 15 km from Bafia, road Bafia-Ndikinimeki, 16 August 1960, *Mpom, B. 402* (P); along Sanaga river, near ferry Nachtigal, c. 20 km N of Obala, 1 July 1964, *Wilde, W.J.J.O. de 2785* (B, BR, EA, FHI, K, MO, P, PRE, WAG, YA, Z); **East Province**: 14 km NE of Doumé, or 9 km SW of sawmill near Dimako, S. of road, 5 December 1960, *Breteler, F.J. 724* (BR, K, LISC, M, P, SL, UC, WAG, YA); N of Moundi, 16 January 1960, *Letouzey, R. 2654* (P, WAG); 3 km of Momjepom, 22 km of the road of Yokadouma -Moloundou, 1 June 1963, *Letouzey, R. 5199* (P); near Mwapak (43 km on Yokadouma-Lomie road), 17 June 1963, *Letouzey, R. 5293* (G, P, WAG); Molundu, 4 December 1910, *Mildbread, G.W.J. 4090* (WAG);

CENTRAL AFRICAN REPUBLIC: Lobaye: Bambari, *Tisserant, C. 622* (P); Mabaiki, Boukoko, 26 August 1947, *Tisserant, C., Equipe 159* (P); Region of Mbaiki and Boukoko, *Tisserant, C., Equipe 1007* (P); Mbaiki and Boukoko region, Boukoko station, 10 October 1948, *Tisserant, C., Equipe 1188* (BM, WAG); **Ombella Mpoko**: Bangui, 18 December 1903, *Chevalier, A. 10847* (P);

CONGO (BRAZZAVILLE): Bouenza: Moyen Congo, Jokeni near Mouyondzi, 21 Jan. 1954, *Koechlin, J. 2453* (P);

CONGO (KINSHASA): Bas-Congo: Lombo, (Terr. Thysville), 8 November 1959, *Compère, P. 806* (BR); road Kimpese to Songa, 16 June 1960, *Compère, P. 2150* (BR); Prov: Léopoldville, Territ. Boma, Luki, 2 July 1948, *Donis, C. 1882* (BR, WAG); Prov: Léopoldville, Territ. Thysvlle, M'vuazi, 11 June 1957, *Dubois, J. 191* (BR, MO); Kenge, 2 November 1979, *Nsimundele 628* (BR); Gimbi, Source of the Fuka river, 31 December 1948, *Toussaint, L. 711* (BR); Congo da Lemba, October 1913, *Verschueren 750* (BR); **Equateur**: station Inéac Boketa, 3 March 1955, *Evrard, C. 349* (BR); Bosambala, 12 April 1955, *Evrard, C. 670* (BR); Station INÉAC Boketa, 19 April 1955, *Evrard, C. 728* (BR); Popolo, along Mangala?, 10 August 1955, *Evrard, C. 1603* (BR); **Katanga (Shaba)**: Kaniama, Luba Gallery, Kitengia, September 1935, *Herman 2117* (BR); **Maniema**: 60 km on road Kasongo-Kindu, June 1952, *Germain, R. 7835* (BM, YBI); **Orientale**: Irumu, 12 March 1914, *Bequaert, J.C.C. 2952* (BR); Sokudi, along Neduwe, 21 June 1942, *Dubois, H. 162* (BR); Bambeto, 1943, *Dubois, H. 912* (BR, YBI); Bambeto, 1942, *Dubois, H. 955* (BR, YBI); Bambeto, 1943, *Dubois, H. 998* (BR, YBI); Ango area, source of Bili, December 1945, *Germain, R. 4390* (BR); Irumu, Mont Homas, July 1949, *Germain, R. 5308* (BR); Madengedenge, August 1937, *Gilbert, G. DiFor 255* (BR); Prov: Orientale, Territ. Mangbetu, Paulis, February 1939, *Gilbert, G. 2092* (BR, NY, WAG); Yangambi Reserve forest, 1949, *Gilbert, G. 9126* (BR); Yangambi, 1949, *Gilbert, G. 9309* (BR); Station Epulu, Mambasa, 23 March 1981, *Hart, T.B. 16* (BR); Mambasa Zone (Ituri forest), 15 April 1991, *Hart, T.B. 1122* (MO); Epulu, Zone of Mambasa, 15 June 1991, *Hart, T.B. 1151* (BR); Mambasa (Ituri forest), 7 April 1993, *Hart, T.B. 1536* (MO); Kawa forest, 28 September 1955, *Smeyers, F. 311* (BR); **Unknown**: Lac Albert, gallery forest of Kawa, 19 March 1954, *Ben, D. van der 1259* (BR); Massif Vunda, 16 September 1954, *Dubois, J. 59* (BR);

EQUATORIAL GUINEA: Annobon Island: Annobon Island: between Capelle San Juan & San Pedro, 21 July 1959, *Wrigley, T.C. 68* (BM); **Bioco (Fernando Poo)**: Malabo-Luba, estrada km 11, 32NMK6911, 21 July 1986, *Carvalho, M.F. de 2040* (MA, WAG); Bioco, Malabo Riaba, 58 km of the road, 29 May 1987, *Carvalho, M.F. de 2936* (NY, P); Malabo-Baney, 17 km on the coast road, 7 July 1988, *Carvalho, M.F. de 3519* (MA, MO, WAG); Malabo-Baney by the coastal road, km 17, 1991, *Fernández Casas, F.J. 233429* (G);

ETHIOPIA: Illubabor: Tepi, March 1977, *Chaffey, D.R. 1241* (K); Illubabor Province, about 7 km NW of Tippi airstrip, 14 January 1962, *Meyer, F.G. 8007* (K); near first stream crossing after leaving Teppi, Mesan Teferi trail, 12 November 1964, *Meyer, F.G. 8929* (P, US, WAG); **Kefa:** Kefa A. Region: At the Bebeka coffee Plantation, on the way to the hot springs, about 25 km west of the coffee plantation, 30 November 1984, *Friis, I. 3887* (C, K);

GABON: **Nyanga**: forêt du Mayombe bayaka. Tchibanga, 13 November 1909, *Le Testu, G.M.P.C. 1479* (P, WAG); Tchibanga, January 1915, *Le Testu, G.M.P.C. 1965* (P); Forest in savannah, c. 30 km S of Doussala, 23 October 1985, *Reitsma, J.M. 1741* (WAG); Réserve de Monts Doudou, SW of Brigade de Moukalaba à Morindi, 20 March 2000,

Sosef, M.S.M. 875 (LBV, WAG); 25 km SSE of Doussala, forest gallery along small river, 14 March 1988, *Wilde, J.J.F.E. de 9349* (WAG); **Ogooué-Lolo**: Bambidie, axe Lastoursville-Ndangui, 21 May 2003, *Nziengui, B. 521* (LBV, WAG); **GHANA: Brong-Ahafo Region**: Near Kwapon, about 100 km WSW of Kumasi, 18 December 1963, *Oldeman, R.A.A. 739* (B, BR, FHI, K, LD, MO, P, WAG); **Eastern Region**: Apedwa Forest Reserve, 28 June 1994, *Jongkind, C.C.H. 1617* (MO, WAG); **Unknown**: Akrum river, near Aketswia, 11 June 1970, *Hall, J.B. 39638* (GC, MO); Abetifi-Aduamoa road (Eastern Region), January 1932, *Irvine, F.R. 1729* (E);
IVORY COAST: Bouaké: Bouaké, 9 October 1949, *Adam, J.G. 6428* (MO); **Bouna**: 9 km N of Kakpin, 18 April 1968, *Geerling, C. 2530* (WAG); 9 km N of Kakpin, 18 April 1968, *Geerling, C. 2539* (WAG); P.N. Comoé Sud, 20 May 1990, *Poilécot, P. 2823* (G; not seen!); P.N. Comoé Sud, 15 August 1988, *Poilécot, P. 4368* (G; not seen!); **Daloa**: 8-10 km E of Daloa, 5 March 1962, *Bernardi, L. 8483* (WAG); **Daoukro**: km 11 road Daoukrou-Ananda-Kouassikro, 5 December 1968, *Breteler, F.J. 6188* (B, BR, C, FHI, FHO, GC, K, LE, MO, PRE, US, WAG); **Séguéla**: Vavoua, vers Séguela (village), 19 October 1949, *Adam, J.G. 6674* (MO); Séguela, 23 October 1968, *Dugerdil, M. 533* (G; not seen!); **Unknown**: 1932, *Aubréville, A. (Ivory Coast series) 939* (P, WAG); Lamto. Forêt du grand nord, 15 February 1990, *Chatelain, C. 103* (G, LAMTO); Lomo-Sud, 26 October 1990, *Chatelain, C. 366* (G); Haut Sassandra, pays des Dyolas, between Droupleu and Zoanlé, 5 May 1909, *Chevalier, A. 21459* (BR); Morénou, environs de Akabilikrou, 6 December 1909, *Chevalier, A. 22511* (P, WAG); Lamto, 10 June 1975, *Devineau, J.-L. 1210* (LAMTO; not seen!); Lamto, 27 October 1987, *Gautier, L.; Béguin, D. 654* (CSRS, LAMTO; not seen!); Lamto, January 1972, *Spichiger, R. 273* (CSRS, LAMTO; not seen!); Lamto, 12 March 1975, *Vuattoux, R. s.n.* (LAMTO; not seen!); **Vavoua**: F.C. du Haut-Sassandra, Nord, entre layon 1et limite Nord, 21 September 1993, *Kouamé, F.N. 581* (CSRS; not seen!); F.C. du Haut-Sassandra, Centre, forêt très dégradée, relevé FNK25, 2 March 1995, *Kouamé, F.N. 1420* (CSRS; not seen!);
KENYA: Coast: Kwale District, 15 miles SW of Kwale, 27 August 1953, *Drummond, R.B. 4014* (BR); Kwale district, Mrima hill, 5 March 1977, *Faden, R.B. 77/ 701* (K); **Unknown:** 7 km NE of Garsen, 16 July 1972, *Gillett, J.B. 19944* (FI); Kenya, Mrima Hills- Rainforest, 25 June 1970, *Hansen, O.J. 100* (C);
NIGERIA: Cross River State: Province: Ogoja, Distict: Obubra, 25 August 1960, *Adebusuyi, J.K. FHI 43980* (FHI, WAG); **Enugu State**: 11 miles on Abakaliki-Obubra road, Izicha, 27 February 1973, *Okafor, J.C. FHI 66035* (WAG); **Ogun State**: West District, Abeokuta, Olokemeji, 6 May 1975, *Gbile, Z.O. FHI 73656* (WAG); Olokemeji forest Reserve; 32 km W of Ibadan, 14 June 1981, *Gentry, A.H. 32662* (K, MO, WAG); Road from Ilaro to Abeokuta, about 2 km N of Ilaro (Western State, Abeokuta Province), 12 May 1968, *Meer, P.P.C. van 763* (WAG); **Ondo State**: Dist: Ekiti, Omuo Forest, 3 March 1973, *Olorunfemi, J. FHI 70699* (FHI, WAG); Okeluse F. R. disused hauling road, 22 July 1953, *Onochie, C.F.A. FHI 33362* (FHI, K, P); **Osun State**: Shasha Forest Reserve, 35 km ENE of Ondo (Western State, Oyo Province), 10 July 1968, *Meer, P.P.C. van 820* (WAG); **Oyo State**: Ibadan, Campus of university, *Gurk, D.P.M. 2700* (FHI); Ibadan Prov., about 10 miles W of Ijaiye, about 21 miles NW of Ibadan. In forest edge on laterite, along track, 5 March 1968, *Meer, P.P.C. van 652* (WAG); **Taraba State**: Adamawa Prov, Gangumi, on the second line from the base line, 11 December 1954, *Latilo, M.G. FHI 28885* (K, P); **Unknown**: Valley between Olurere and Orosun peaks, 5 January 1948, *Brenan, J.P.M. 8718* (K, P); Lokomedji, July 1905, *Chevalier, A. 14071* (P); Aponmu forest reserve, 9 August 1962, *Gillett, J.B. 15323* (K, P); Oleoruta prov., 20 May 1945, *Oladoyinbo, A. 8224* (FHI, K, P);
SENEGAL: 7 km E of Kayar, east bank of Tanma Lake, 1 km SE of Ntiaye, 24 June 1961, *Raynal, J. 7105* (P);
SUDAN: **Eastern Equatoria**: Equatoria Province, Torit District, 6 April 1950, *Jackson, J.K. 1385* (K);
TANZANIA: **Morogoro**: Morogoro Rural District, Ngambaula forest Reserve, 22 August 2000, *Mhoro, B. 407 A* (MO); **Unknown**: Prov. Tanganyika, 29 December 1960, *Semsei, S.R. 3139* (K, P);
TOGO: Plateaux: Coetonou, km 92 Lomé - Avétonou, 17 September 1971, *Breteler, F.J. 7172* (B, BR, FHI, FHO, HBG, MO, P, PRE, US, WAG); **Unknown**: 6 km E of Tsévié, 20 November 1977, *Ern, H. 2483* (P, TOGO);
UGANDA: June 1917, *Dümmer, R.A. 3046* (BM); Waisoke River, Budongo forest, September 1933, *Eggeling, W.J. 1422* (K); **Western Province**: Budongo forest, Kaniyo-Pabidi beat, February 1996, *Hafashimana, D.L.N. 15* (C); N. Bunyoro, Bujenje, Budongo forest, 14 September 1977, *Katende, A.B. 2739* (MO); Budongo Forest Reserve. Nature Reserve, close to the Sonso River, forest dominated by *Cynometra alexandri* and *Khaya anthotheca*. Along trail, 20 August 1995, *Nkuutu, D.N. 6- 16* (C); Bunyoro District, 24 September 1962, *Styles, B.T. 65* (FHO, K).

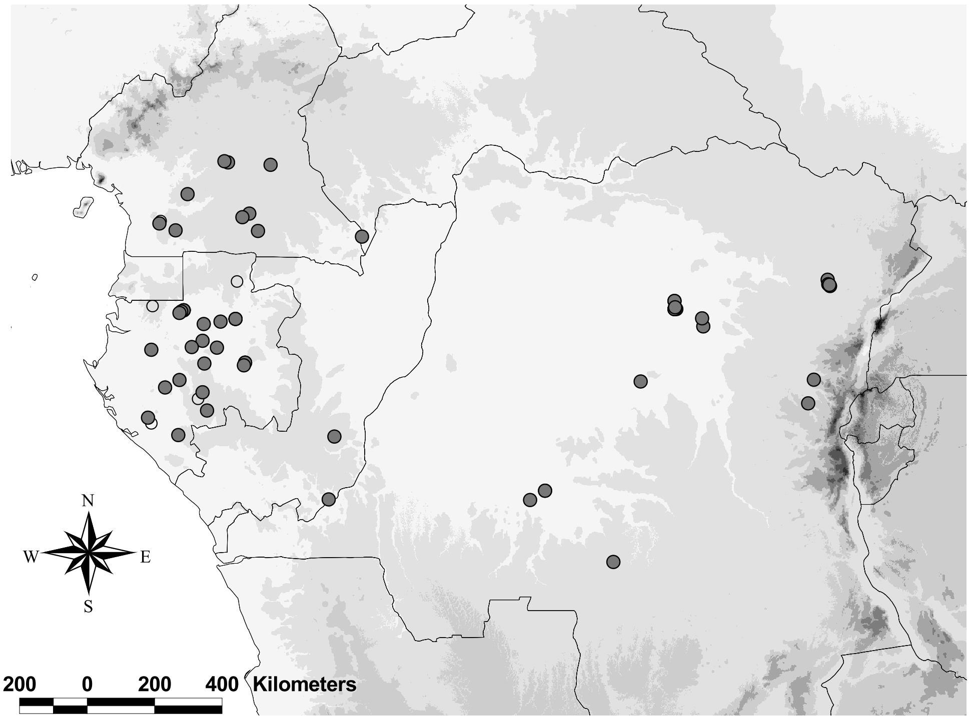
9. *Celtis tessmannii* Rendle.

Journ. Bot. 53 (1915) 297; & Fl. Trop. Afr. 6 (2): (1916); Polhill, Kew Bull. 19 (1964) 140; Fl. Cameroun 8 (1968) 44. Type: from Equatorial Guinea: inland, Mabungo 450 m, *Tessmann B25* (isotype: K!).

Synonyms:
Celtis brieyi De Wild., Miss. de Briey: 3 (1920); Hauman, Fl. Congo belge 1 (1948) 46, tab.7 ; De Saint Aubin, Foret Gabon (1963) 189. Type: Congo Kinshasa, Region of Ganda-Sundi, *Briey 152* (holo: BR).

Tree, 30-40 m tall, 80-100 cm diameter, trunk cylindric, bark dark greyish, with patches of light grey, rough, crown conical, branches spread out, wavy, much branched, leaf blades entire, alternate, elliptic, 4-9 cm long, 2-4 cm wide, strongly unequal at the base, sharply acuminate and apiculate at the tip, main nerves 3 from the base, 2-3 each side of the midrib, anastomosed (merged) in an bow before reaching the margin;blade sparsely and shortly hairy both sides, Scabrous, more so on the veins than on the rest of leaf, petiole 4 mm long.Stipules caducous, lanceolate-linear, up to 4 mm long. Cymes 4–15 mm long, of many, rarely few, often crowded male flowers with pedicels up to 4 mm long, hermaphrodite flowers 1 or few at the apex of the cyme, uppermost flowers, sepals 5, 1.5–2 mm long, pubescent. Ovary shortly and densely hairy with two broadened stigmata, deeply divided. Fruit a drupe, globose, 10-15 mm long, 8-12 mm wide, orange to black, endocarp 11x10mm, lenticular, polygonal, rough. Pollen grains triporate and problate spheroidal.

Distribution: Gabon, Cameroon, Congo Kinshasa (map 7.9).
Habitat and ecology: Rain Forest (200-700 m).



Distribution map 7.9. *Celtis tessmannii* in Africa.

Specimens examined:

***Celtis tessmannii* Rendle**

CAMEROON: **Central Province**: 9 km from Yaoundé, road to Makak, path to Eloumden, 20 October 1961, *Breteler, F.J. 1975* (A, BR, FI, K, LISC, M, P, SL, UC, WAG, YA); Essam, 13 February 1959, *Letouzey, R. 1296* (P); Essong Forest (IGN sheet Nanga Eboko), 8 May 1959, *Letouzey, R. 1882* (P, WAG); **East Province**: 4 km N of Bertoua, road to Deng-Deng, 31 August 1961, *Breteler, F.J. 1808* (BR, FI, K, LISC, M, P, WAG, YA); SW of Ndinge, Abong-mbang, April 1961, *Letouzey, R. 3845* (P); 12 km S of Djouo (20 km E of Somacomo), 23 February 1962, *Letouzey, R. 4337* (P); Dja faunal reserve, Alat-Makay, 14 July 1995, *Sonké, B. 1630* (BR, YA); **South Province**: Ngongondje hill, near Akonetye, S of Ebolowa, 28 August 1978, *Koufani, A. 125* (P); 1500 m S of village d'Ebom, piste villageoise, 8 August 1996, *Ndoum, D. 56* (KRIBI, WAG); about 7 km NE of Ebom. Plot 9, subplot 83, tree 5, coordinates: X = 7.5, Y = 7.5 m, August 1996, *Parren, M.P.E. 132* (KRIBI, WAG);

CENTRAL AFRICAN REPUBLIC: **Sangha Economique**: Lindjombo, within 3 km of village, 15 November 1988, *Fay, J.M. 8833* (MO, WAG);

CONGO (BRAZZAVILLE): **Plateaux**: Bafuru plateau, 2 km N of Ontchouo village, 19 October 1991, *Thomas, D.W. 8663* (MO);
CONGO (KINSHASA): **Equateur**: Region of Equateur, zone Ikela, road Lokofe-Ikumaloki, village Balanga, north of Tshuapa River, *Bermejo, M. 94* (BR); **Kasai Occidental**: North of Lutshuadi, September 1953, *Deffet 16 J* (BR); Kamembele (Territoire Dibaya), *Liben, L. 2254* (BR); **Kinshasa**: Nioki, July 1941, *Flamigni, A. 9010* (BR, P, WAG); **Nord-Kivu**: Luka River, *Michelson, A. 260* (BR); km 153 road of Sake-Walikale, 10 June 1958, *Pierlot, R. 2185* (BR); **Orientale**: Yangambi, 1949, *Gilbert, G. 9602* (BR); Yangambi, area Plateau, 1947, *Gilbert, G. 10116* (WAG); Zone of Mambasa (Ituri). Epulu, 31 March 1987, *Hart, T.B. 712* (MO); Epulu, zone of Mambasa (Ituri forest), 10 May 1991, *Hart, T.B. 1128* (MO); Afarama, zone of Mambasa (Ituri forest), 18 March 1992, *Hart, T.B. 1360* (MO); Zone of Mambasa, (Ituri forest) Afarama, 28 July 1992, *Hart, T.B. 1374* (BR); 70 km of Kisangani, 19 October 1973, *Lisowski, S. 16385* (K); Yangambi, km 8 road of Ngazi, 11 December 1937, *Louis, J. 800* (NY, WAG); Yangambi, 25 March 1937, *Louis, J. 3493* (BR, C); Yambao, 25 km of N-W of Yangambi, 17 March 1937, *Louis, J. 3622* (BR); Yangambi, 16 May 1952, *Louis, J. 3830* (BM, BR); Yangambi, 4-8 km of north of hillslope of Luweo, Reserve of Lusambila, 19 March 1937, *Louis, J. 3908* (BR); Yambao, 25 km NW Yangombi, 17 March 1937, *Louis, J. 5622* (BR, C); Yangambi, 8 km of Ngazi road, 23 July 1937, *Louis, J. 5633* (BR, C, MO); Yangambi, Isalowe flora reserve, 2 November 1937, *Louis, J. 6478* (BR, NY); km 25 C.F. L. Ier Trongon Stanleyville, 12 March 1939, *Meiren, J.J. van der 60* (BR); **Unknown**: Sanguru, February 1906, *Luja, E. s.n.* (BR); Sanguru, July 1903, *Luja, E. s.n.* (BR);
GABON: **Moyen-Ogooué**: environs de Nkogo, sur l'Ogooué, 22 August 1912, *Chevalier, A. 26618* (BR, P, WAG); **Ngounié**: Boutoumbi, November 1925, *Le Testu, G.M.P.C. 5737* (P, WAG); Mouyanama à 25 km de Mimongo en allant vers Mbigou à ± 40 minutes à pied en allant vers le village Ibaga, 12 February 1990, *Louis, A.M. 3160* (LBV; not seen!); 15 km on the road Mbigou to Malinga, 9 December 2001, *Wieringa, J.J. 4665* (LBV, WAG); upper Waka area, 11 km on IFL forestry road B2, 28 March 2004, *Wieringa, J.J. 5101* (WAG); 6 km on Rimbunan Hijau forestry road 2-1, 3 April 2004, *Wieringa, J.J. 5225* (WAG); **Nyanga**: Secondary forest along exploitation road ± 40 km SW of Ndendé, 2 December 1983, *Louis, A.M. 1105* (WAG); **Ogooué-Ivindo**: M'passa, 2 May 1977, *Florence, J. 217* (P); M'passa, 5 April 1978, *Florence, J. 824* (P); 5km S of Petit Okano, 21 March 1979, *Florence, J. 1914* (P); M'passa, 26 May 1979, *Florence, J. 2070* (P); Forêt des Abeilles, 15 km SE du confluent Ogooué -Ivindo, 2 April 1984, *Wilks, C.M. 894* (LBV, WAG); 20 km N of Koumameyong, 17 March 1987, *Wilks, C.M. 1417* (MO, WAG); 4 km E of Agnang, 10 May 1989, *Wilks, C.M. 1922* (MO, WAG); Lopé Reserve, 1986, *Williamson, E.A. 17* (K); **Ogooué-Lolo**: about 30 km E of Lastoursville, 19 November 1991, *Breteler, F.J. 10580* (WAG); about 30 km E of Lastoursville, 30 November 1991, *Breteler, F.J. 10838* (WAG); Makande surroundings, about 65 km SSW of Booué, Makande, 27 February 1999, *Breteler, F.J. 15243* (LBV, WAG); Bambidie, about 30 km E of Lastoursville. Permanent plot at Bambidie Station, Plot 6, 6 November 1999, *Breteler, F.J. 15376* (LBV, WAG); **Ogooué-Maritime**: ± 17 km sur la route à partir de Doussala NW direction, 23 March 2000, *Sosef, M.S.M. 1376* (LBV; not seen!); old logging road leading southward from chantier CBG Peni, 22 April 2005, *Valkenburg, J.L.C.H. van 3165* (BR, LBV, WAG); **Unknown**: October 1993, *McDonald, K.E. 65* (E); **Woleu-Ntem**: Region between Ogooué and Cameroon, Essona, November 1933, *Le Testu, G.M.P.C. 9366* (P, WAG); Minkébé area, 1747 m on transect A, 8 March 1990, *Minkébé Series W 36* (WAG; not seen!); Crystal Mountains, 50 m on transect G1, 5 July 2001, *Obiang Mbomio, D. 167* (LBV; not seen!); Inventory Oveng; primary rain forest, c. 25 km WSW of Mintsic, 5 November 1986, *Reitsma, J.M. 2483* (WAG); Inventory Oveng; primary rain forest, c. 25 km WSW of Mintsic, 6 November 1986, *Reitsma, J.M. 2497* (NY); Chantier Oveng; primary rain forest, c. 25 km WSW of Mintsic, 9 November 1986, *Reitsma, J.M. 2569* (WAG); Chantier Oveng; primary rain forest, c. 40 km W of Mintsic, 10 November 1986, *Reitsma, J.M. 2592* (WAG);

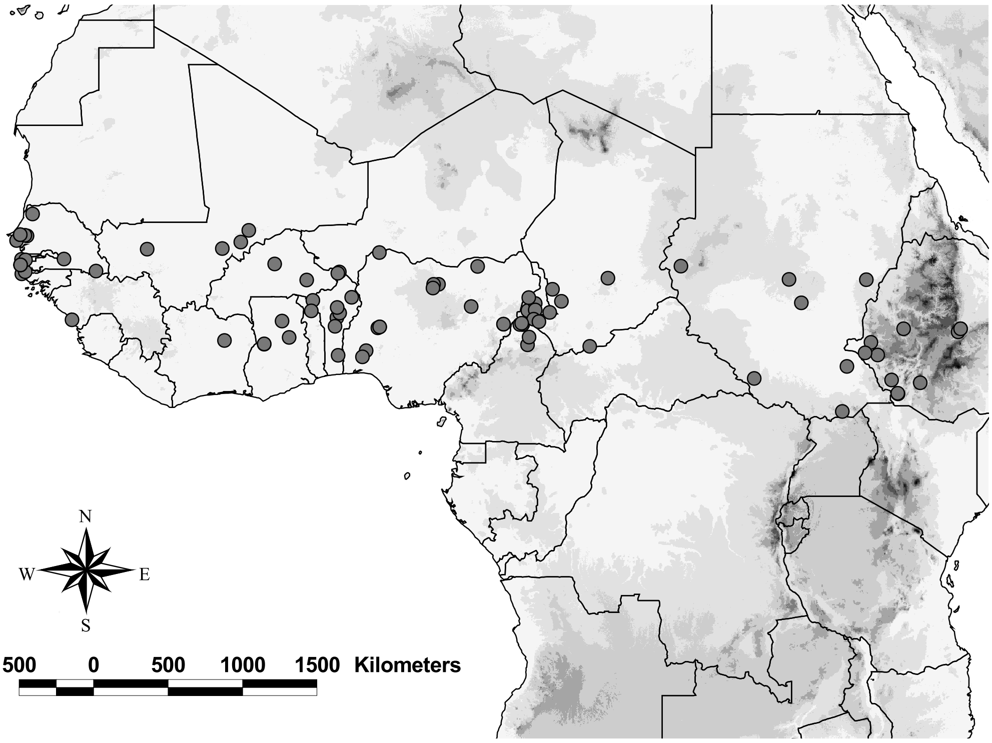
10. *Celtis toka* (Forssk.) Hepper & J. R. I. Wood

Encycl. meth. Bot. 4 (1797) 140; Planch., in DC., Prodr. 17 (1873) 192; Kew Bull. 38 (1983) 86; Engler, Pflanzenw. Afr. 3(I) tab. 6A (1915) 14; Rendle, FTA 6, 2 (1916) 7; Vaillant, Bull. Soc. Etud. Camer. 9 (1945) 40; Aubreville, Andrews, Flow. Pl. Anglo-Egypt. Sudan 2 (1952) 251 tab. 87; Sillans, Mém. Soc. Bot. France (1952) 103; Cufondontis, Bull. Jard. Bot. Etat 23, suppl.: 5 (1953) Keay, FWTA ed. 2, 1(1958) 592, tab. 171; Aubreville, Fl. For. Cote d'Ivoire 1, 3-4 (1959) 39, tab. I; Keay, Onochie & Stanfield, Nigerian trees 2 (1966) 156, tab. 116 D; Berhaut, Fl. Senegal ed. 2 (1967) 231; Kew Bull. 38 (1983) 86.

Synonyms: *Ficus toka* Forssk., Fl. Aegypt.-Arab 219 (1775); type: none extant;
C. integrifolia Lam., Encycl. 4 (1797) 140, Fl. W. Trop. Afr. ed. 2, 1 (1958) 592. Type: Senegal, *Adanson 229A* (holo: P; photo: K!).

Tree, 15-25 m tall, deciduous, monoecious, narrow buttresses; bark light grey, smooth or scaly, young twigs pubescent. Leaf blades broadly ovate, 5--7cm long, 2--4 cm wide. shortly acuminate, rounded to subcordate at the base, unequal-sided, entire, scabrous, subglabrous with a few hairs on the veins beneath and in the vein-angles, 3-nerved from the base, with the basal lateral nerves ascending well into the upper half of the leaf, and the upper prominent lateral nerves 1-3 on each side of the midrib; petiole 4--6 mm long. Stipules linear, 4--5 mm long, pubescent. Cymes 2--4 cm long in flower, and up to 5 cm in fruit, axillary or at the nodes below, with many clustered male flowers and with several terminal hermaphrodite flowers, Sepals 4--6, 3-5 mm long pubescent. ovary shortly pubescent with a ring longer hairs at the base, styles2--3 branched, 3--5 mm long, fruit a drupe, globose, 8--11 mm long, 7--10 mm, brownish to balckish, scabrous, endocarp 7x6 mm, ovoid, polygonal, rough. Pollen grains triporate, oblate-spheroidal.

Distribution: From Senegal to Uganda and Sudan (map 7.10).
Habitat and ecology: Dry areas, savanas, along rivers (100-500 m).



Distribution map 7.10. *Celtis toka* in Africa.

Specimens examined:

***Celtis toka* (Forssk.) Hepper & J.R.I.Wood**

BENIN: **Atacora**: Gouandé, 17 August 2000, *Essou, J.-P. 2387* (BENIN, WAG); Sérou, 20 August 2001, *Essou, J.-P. 2679* (BENIN, WAG); **Borgou**: 15 June 1998, *Adjakidjè, V. 1841* (BENIN, WAG); Tchatchou, 11 April 1999, *Akoègninou, A. 2378* (BENIN, WAG); Toumè, 11 August 1999, *Akoègninou, A. 2816* (BENIN, WAG); Sonoumon, 20 March 2001, *Akoègninou, A. 4459* (BENIN, WAG); *Houngnon, P. 2816* (BENIN, BRLU, WAG); 30 April 1999, *Houngnon, P. 6629* (BENIN, WAG); Bétérou, 19 April 2000, *Houngnon, P. 7612* (WAG); Few km W of Sonouhon, 17 March 2002, *Maesen, L.J.G. van der 7703* (BENIN, WAG); **Ouémé**: Aguigadji, Forêt Classée de Kétou, along Ouémé river, 27 November 1998, *Maesen, L.J.G. van der 6728* (BENIN, WAG);

BURKINA FASO: **Gourma**: Route Fada N'Gourma-Namoungou, 2 November 1994, *Monsch, K.A. 91* (WAG); **Sanmatenga**: road of Kaya to Malou, 17 km W of Kaya, 14 August 2005, *Maesen, L.J.G. van der 8219* (CNSF, WAG);

CAMEROON: **North Province**: Mogazin Hill, 10 km NE of Maroua, 23 September 1964, *Biholong, M. 157* (P, WAG); Garoua-Guidder, km 20, 11 February 1953, *Bounougou, E. 4544* (P); North -Cameroon, 10 December 1954, *Bounougou, E. 4545* (P); Djengreng (C. Bongor), 12 January 1968, *Gaston, A. 1466* (P, WAG); km 27 of road Garoua-Rey Bouba, E of Pitowa, N of Mayo Kébi, a tributary of the Benoué R., 28 January 1966, *Leeuwenberg, A.J.M. 7603* (B, BR, C, COI, DES, EA, FHI, GENT, HBG, K, L, LD, LG, LISC, LUAI, MHU, MO, P, PR); near Moutouroua (45 km SSW of Maroua), 'Colline de l'Aiguille Messengel', 28 August 1964, *Letouzey, R. 6513* (P, WAG); National park of Bénoué (campement du Grand Capitaine) 25 km, SSE of Garoua, 11 April 1981, *Meijer, W. 15521* (MO, WAG); Mousgoy (Distr. Guider), 29 April 1964, *Sammicheli, A. s.n.* (FI); Garoua, 5 August 1955, *Wit, H.C.D. de 7932* (WAG); Benoué National Park, 2 km E of Buffle Noir Camp, 3 October 1974, *Wit, P. 2928* (WAG); 8 km after Pitoa on road from Rey to Bouba, 29 June 1975, *Wit, P. 3114* (WAG); National Park of Mozogo-Gokoro, Mayo Ngassawe, eastern, 16 July 1981, *Zon, A.P.M. van der 1042* (WAG);

CHAD: **Mayo Kebbi**: Mayo-Kebbi, 1 September 1984, *Lisowski, S. B 640* (BR); **Unknown**: Ba-llli, 4 March 1969, *Fotius, G. 1373* (P); Narrow valley near Chari, 26 July 1969, *Fotius, G. 1626* (P); Léré, along lake, 2 March 1971, *Gaston, A. 2930* (P, YA); 82 km S of N' Djamena, Bougoumen village, 5 August 1984, *Lisowski, S.B. 109* (BR); c. 10 km S of Mongo, 10 January 1965, *Wilde, W.J.J.O. de 5287* (WAG);

ETHIOPIA: **Gamu-Gofa**: Lake of Murle, 19 July 1939, *Corradi, R. 8321* (FI); bank of Dell' Omo, Murle, 16 July 1939, *Corradi, R. 8324* (FI); Gamu-Gofa Region: Lower Omo Valley, at Russo's camp (Karo), 13 November 1998, *Friis, I. 9010* (C); **Illubabor**: Gambela, capital of Illubabar Province, 24 July 1971, *Ash, J.W. 1076* (K); **Unknown**: Zone N of Lekemti, gurracci, 21 June 1947, *Capuano, D. 19* (FI); SW Omo valley Expedit ION, Lower Omo River Basin, August 1970, *Carr, C.J. 899* (MO); between Punido town and Gilo River, small Forest Island on the bank of River, 22 November 1995, *Friis, I. 7262* (BR); 2-3 km S of Abobo, 20 April 1982, *Friis, I.; Vollesen, K. 2479* (C); Awash valley, 4 miles west of Metahara, along Awash River, 19 August 1968, *Headley, P.M. 228* (K); Awash valley, 20 December 1968, *Longhitano, N. 4* (FI); Yerer, Kereyou Awraja, Awash National Park c. 5-7 km from the camp northward following Awash river, 15 January 1986, *Sebsebe Demissew 1709* (C);

GAMBIA: Kombo, 1835, *Heudelot, J. 104* (P); **Western Division**: W. D. Kombo east district.Bama Kuno Forest park, 12 March 1995, *Descheres, K. 53842* (BR); Abuko Nature Reserve, July 1979, *Starin, E.D. 1* (K);

GHANA: **Brong-Ahafo Region**: Bamboi, 17 January 1996, *Jongkind, C.C.H. 2594* (LISC, P, WAG); near Bamboi (N.T.), May 1935, *Vigne, C. FH 3840* (BM); **Northern Region**: Kurumbugu, 17 May 1927, *Kitson, A.E. 750* (K); **Unknown**: Salaga, N Territory, *Dalziel, J.M. 13* (E, K);

GUINEA: **Conakry**: near Conakry, Ogogoro, 26 September 1955, *Wit, H.C.D. de 7089* (WAG);

IVORY COAST: **Dabakala**: Dabakala, near creek, on sandy soil, 13 February 1968, *Geerling, C. 2005* (WAG); **Unknown**: May 1939, *Aubréville, A. (Ivory Coast series) 3006* (P);

MALI: **Kayes**: Parc National de la Boucle du Baloué. 4 km W of Dyontégéda, bank of Baloué river, 20 January 1979, *Dekker, A.J.F.M. 352* (WAG); **Unknown**: near Dourou town, 19 August 1990, *Aké Assi, L. 18166* (G); Miake near Djenne, 30 June 1899, *Chevalier, A. 1136* (WAG); Douentza, *Jaeger, P. 5401* (C);

NIGER: **Niamey**: Park "W" Niger, 4 October 1975, *Hempe, J. 90* (MO); Park W, road Embarcadere, at the Niger River, 27 February 1977, *Mazurski, M. 34* (K, MO);

NIGERIA: **Adamwara State**: Zing in the Mumuye country, between Mayo Belwa and Valingo, 8 September 1974, *Chapman, J.D. 3353* (K); State: North-East, District: Adamawa, Locality: Yola, Proposed Adamawa, 24 October 1971, *Latilo, M.G. FHI 63523* (FHI, WAG); **Bauchi State**: Bauchi, March 1929, *Lely, H.V. 182* (K); **Kano State**: 25 miles S of Kano, 8 July 1972, *Blom-van Teyn, M. van 153* (WAG); Kano, Wudil District Wudil District of Kango state, located approximately 50 km SE of the city of Kano, 11 November 1987, *Etkin, L. 199* (MO); N Nigeria, Rano, Zuwo, November 1979, *Sharland, R.E. 967* (K); **Kwara State**: Jebba, 9 December 1927, *Hagerup, O. 687* (C); Niger Valley, 10-20 km down stream of Jebba, April 1960, *Kamphorst, A. 13* (WAG); Nigerdal, 10-20 km down town of Jebba, 1 April 1960, *Kamphorst, A. 33* (C, WAG); **Oyo State**: Ibadan, Prov, Oyo, 27 March 1962, *Bernardi, L. 8835* (G); Oyo to Fiditi, 20 April 1968, *Gledhill, D. 994* (WAG); **Sokoto State**: Manu. N Nigeria, 19 March 1915, *Foster, E.W. 5* (K); **Unknown**: Katagum district, March 1908, *Dalziel, J.M. 213* (K); Majurjour Lakes, Kurmis, near Magori Lake, December 1960, *Leeuw, P.N. de 45* (WAG);

SENEGAL: **Casamance**: Kafountine, 11 September 1984, *Vanden Berghen, C. 6339* (BR); Kafountine, near Île aux Oiseaux, Vegetation survey 1003, 4 August 1989, *Vanden Berghen, C. 9014* (BR); Kafountine, near Île aux Oiseaux. Vegetation survey, 6 August 1989, *Vanden Berghen, C. 9041* (BR); Basse-Cassamance, Enampor, near village, 10 August 1989, *Vanden Berghen, C. 9071* (BR, MO); **Oriental**: Kédougou, Gambie River, 25 May 1966, *Nongonierma, A. 501* (IFAN, WAG); **Unknown**: Village of Ngue'kor, 1 April 1948, *Adam, J.G. 990* (MO); Thie's, *Adam, J.G. 26855* (MO); Medina Sabak-Nioro, 28 November 1984, *Bamps, P. 7808* (BR); Barkcolgi, Boud mase, 16 January 1964, *Fotius, G. 373* (P); Walo, Mbig[um] in [tivas's], 1839, *Leprieur, F.R. s.n.* (P); *Perrottet, G.S. 711* (P, WAG); Bambey, 13 December 1960, *Raynal, J. 6684* (P); near Diourbel, Diabange Savanna, 20 July 1930, *Trochain, J.L. 13* (P); 19 November 1930, *Trochain, J.L. 917* (P);

SUDAN: **Blue Nile**: E Sudan, Disa, 21 April 1966, *Sahni, K.C. 210* (K); **Darfur Province**: near Sullu, 2 December 1957, *Francis, D. 49* (BM, K); **Eastern Equatoria**: Mt. Imatong and surroundings, 1 km S of Lafon, 28 December 1983, *Kielland 506* (C); **Jonglei**: Gebel Lothir, Pibor Post road, 11 February 1930, *Simpson, N.D. 7523* (K); **Southern Kordofan**: Anglo-Egyptian sudan, near Khor just S of Dilling, 27 January 1934, *Dandy, J.E. 289* (BM); Talodi, Nuba

Mts, 12 April 1930, *Simpson, N.D. 7732* (K); **Western Equatoria**: Inderaabiro, Jebel Marra, 1 April 1965, *Wickens, G.E. 2897* (K);
TOGO: **Unknown**: Naboulgou, 25 December 1977, *Ern, H. 2750* (P, TOGO).

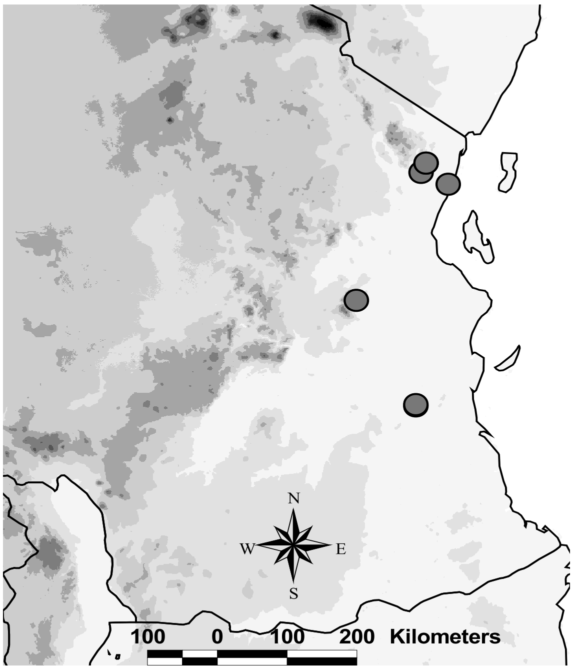
11. *Celtis wightii* Planch.

Ann. Sci. Nat., Sér. 3, 10 (1848) 307; Polhill, Kew Bull. 19 (1964) 141.
Types: India, *Wight 85 & Wight s.n. & Ceylon, Walker 214 & Gardner* (all K, syn.)

Synonyms:
C. mauritiana Planch., Ann. Sci. Nat., sér. 3, 10 (1848) 307; P.O.A.C: 160 (1895); Rendle in Fl. Trop. Afr. 6, 2: (1916) 9; Fl. Deutsch Ost-Afrika-A. 2 (1932) 64; Brenan: 624 (1949) 624; Kenya Trees & Shrubs (1961) 576. Type: Mauritius, Commerson s.n. (holotype: P; isotype: K!); *C. philippensis* Blanco var. *wightii* (Planch.) Soepadmo, Fl. Males. Ser. 1, 8, 2: (1977) 62.

Tree or small tree, 3-20 m tall, often with short shrap buttresses, bark smooth, grey. Young twigs puberulous or subglabrous. leaf blades entire, alternate, coriaceous, elliptic-oblong, 5-8 cm long, 3-7 cm wide, acuminate, broadly cuneate to rounded or subcordate at base, 3-nerved from the base, with the basal lateral nerves extending practically to the near apex and the upper prominent lateral nerves, petiole 4-10 mm long. Stipules lanceolate, 3-7 mm long, shortly produced below the point of attachment, ± pubescent. Cymes 5-30 mm long in flower, up to 40 mm long in fruit, lower ones with many clustered male flowers and hermaphrodite at the top, sepals 5-6, 2-4 mm long, pubescent, ovary glabrous with a basal ring of long hairs, styles shorthly bifurcate, 2-5 mm long. Fruit a drupe, globose, 8-11 mm long, 7-10 mm wide, red to black, endocarp 8x6 mm, ovoid, polygonal, smooth. Pollen grains triporate, oblate-spheroidal.

Distribution: Tanzania, Kenya ? (map 7.11), Sri Lanka, India, South Asia.
Habitat and ecology: margin of the forest, lowland tropics (100-500 m).



Distribution map 7.11. *Celtis wightii* in East Africa.

Specimens examined:

***Celtis wightii* Planch.**

TANZANIA: **Morogoro**: Uluguru Mts, Kimboza Forest Reserva, 4 April 1974, *Faden, R.B. 74/ 414* (MO, WAG); **Tanga**: Muheza, Longuza Forest Reserve, 25 October 1969, *Ngoundai 371* (BR, FI, TFD); Muneza District, Longuza forest, 18 October 1986, *Ruffo, C.K. 1930* (K); Kwamsambia, 20 October 1986, *Ruffo, C.K. 2120* (C, K); Msaraza, Madanga, 17 July 1956, *Tanner, R.E.S. 3006* (K, NY); **Unknown**: T.8. Kingupira Forest, 17 October 1969, *Ludanga, R. 782* (C); T.8 Kingupira Forest, 20 June 1975, *Vollesen, K. 2454* (C).

12. *Celtis zenkeri* Engl.

In Notizbl. Bot. Gart. Berlin. 3 (1900) 22 & Pflanzenw. Afr. 3, 1 (1915) 12; Rendle in Fl. Trop. Afr. 6, 2 (1916) 6; Hauman, Bull. J. Bot. État Brux. 16: 411; Hauman in Fl. Congo-belge 1 (1948) 45; Check-list for trees and shrubs Brit. Emp. 5(2) (1949) 625; Dale & Eggeling, Indig. trees Uganda, ed. 2 (1952) 435 fig. 91a ; Andrews, Flow. Pl. Anglo-Egypt. Sudan 2 (1952) 251; Fl. W. Trop. Afr. ed. 2, 1(1958) 592; Aubreville, Fl. for. Cote d'Ivoire 1 (1959) 39; Taylor, Synecol. Silvic. Ghana (1960) 367 tab. 118; Keay, Nigerian trees 2 (1964) 158; Polhill in Kew Bull. 19 (1964) 141. Type: Cameroon, Yaoundé, 2500 ft, *Zenker & Staudt* 9 (holo: B; iso: P, K).

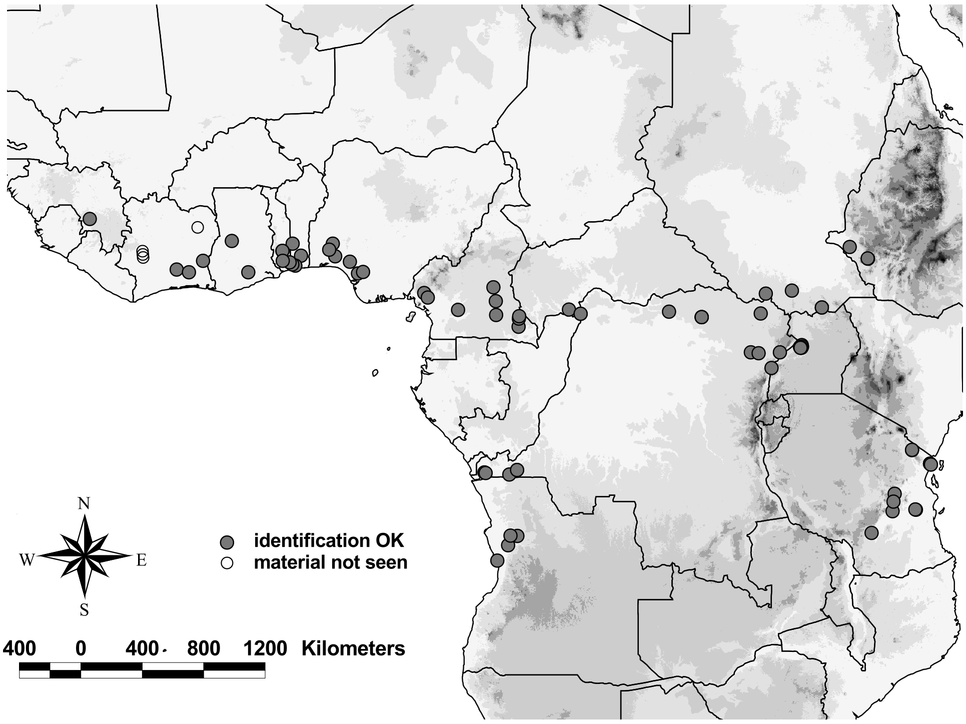
Synonyms:

Celtis soyauxii Engl., Notizbl. Bot. Gart. Berlin 3 (1900) 23. Type: Congo-Brazzaville *Soyaux (Loango-series) 202* (K, lectotype, designated here, see notes); *C. stuhlmannii* Engl. Notizbl. Bot. Gart. Berlin 3 (1900) 23, & Pflanzenw. Afr. 3 (1900) 23, & Pflanzenw. Afr. 3, 1 tab. 9 (B-C) (1915) 14. Type: Tanganyika, Uluguru Mts, *Stuhlmann 8703* (lecotype: B; isotype: K); *C. rugosa* A. Chev., Expl. Bot. Afr. Occ. Franc. 1 (1920) 589. Type : Ivory Coast, Bouroukrou, railroad km 92, 20 Dec. 1906 - 20 Jan. 1907, *Chevalier 16130* & Anoumaba forest, railroad km 140, 12-20 Nov. 1909, *Chevalier 22393* (syntypes: P, not seen; isosyn: BR); *C. affinis* De Wild., Rev. Zool. Afr. 9, suppl. Bot. (1921). Type: Congo Kinshasa, *Bequaert 3301, 3259* (BR, syntypes!).

Tree, 15 - 30 m tall, monoecious, buttressed at the base, bark smooth, grey. Young twigs tawny pubescent to tomentose, leaf blades entire or more rarely toothed in 1/3 upper part, alternate, oblong-elliptic to ovate, 6-13 cm long, 5-8 cm wide, shortly acuminate, apex 6 mm long, broadly cuneate to rounded at the base, glabrous above when mature, hairy especially on the veins, 3-nerved from the base, with the basal lateral nerves extending a little way into upper half, tertiary veins are parallel, petiole 5--8 mm long. Stipules lanceolate 5-7 mm long, pubescent, scarious. Cymes 1--4 cm long in flower up 5 cm in fruit, axillary or at the nodes below, lower ones with many clustered male flowers, often with hermaphrodite flowers, sepals 5-6, 2--3 mm long, pubescent. Ovary densely tawny pubescent, styles 1 or 2 branched, 2--4 mm long. Fruit a drupe, subglobose or ovoid 5--8 mm long, 4-7 mm wide, red or black (at maturity), endocarp 5x4 mm, ovoid polygonal, rough. Pollen grains triporate and sub prolate.

Distribution: West to East and North-East Africa. (map 7.12).
Habitat and ecology: Lowland forest and forest margins (200-800 m).

Note: *Celtis soyauxii* Engl. was based on 4 specimens: two of them, *Soyaux (Loango-series) 202* (K) from Congo, Loango and *Welwitsch 6285* (BM, K) from Angola, Cuanza, are conspecific with *C. zenkeri*, while the other two specimens, both from Angola, Cuanza, *Welwitsch* (*6298* & *6284*) belong to *C. mildbraedii*. Rendle (1916) considered the last two specimens to represent the 'real' *C. soyauxii* but made no choice for a single specimen as lectotype. Following Rendle for about 30 years the name *C. soyauxii* was used for what is here presented as *C. mildbraedii*. However, other authors like Hauman (1942), Keay (1958), Polhill (1964 & 1966) and Letouzey (1968) considered the first two specimens to represent *C. soyauxii*. Neither of these authors established a lectotype, although Hauman (1942) states that Rendle should have had selected *Soyaux 202*. According to article 9.12 of the botanical code (Greuter et al. 2000), the element that corresponds best to the description should be selected as lectotype. In our case this is clearly *Soyaux (Loango-series) 202*, since that element corresponds nearly entirely with the protologue, the only discussion could be on how many dents the leaf margin should have to be “pauciserrata”. *Welwitsch 6298* also fits the protologue fairly well, but is sterile. Therefore we have selected the Soyaux specimen as lectotype, thereby settling the discussion on how to apply the name *C. soyauxii*. *C. soyauxii* was described in the same paper as *C. zenkeri*, but since previous authors regarding them as conspecific have always used the later name, *C. zenkeri* has priority. This priority was probably established by Keay (1958).



Distribution map 7.12. *Celtis zenkeri* in Africa.

Specimens examined:

***Celtis zenkeri* Engl.**

ANGOLA: **Bengo**: Luanda, Caxombo-Quixinge region, 21 January 1971, *Raimundo, A.R.F. 600* (LUA, WAG); **Cuanza Norte**: Golungo Alto, Luinha, 4 October 1907, *Gossweiler, J. 4389* (BM); Mata cafeei de Salazar, 18 November 1968, *Raimundo, F. 19 A* (LUA, WAG); **Cuanza Sul**: Amboim, *Gossweiler, J. 4683* (C, FI); **BENIN**: **Atacora**: Soubouroukou, 29 July 1998, *Akoègninou, A. 1768* (BENIN, WAG); **Borgou**: Tchatchou, 11 April 1999, *Akoègninou, A. 2380* (BENIN, WAG); **Mono**: Avégamè, 5 August 1998, *Essou, J.-P. 832* (BENIN, WAG); Ouèdèmè-Péda, 22 February 1999, *Essou, J.-P. 1552* (BENIN, WAG); Atchannou, 5 July 1999, *Sokpon, N. 852* (BENIN, WAG); **Ouémé**: Ewè, 10 May 1990, *Houngnon, P. 5206* (BENIN, WAG); Pobè, 28 April 1989, *Sokpon, N. B 152* (BRLU; not seen!); **Zou**: Djaloukou (Tchetti), 27 August 2001, *Akoègninou, A. 5329* (BENIN, WAG);

CAMEROON: **Central Province**: Centre agronomique N'Kolbisson, 8 km W of Yaoundé, 24 April 1964, *Wilde, W.J.J.O. de 2299* (WAG); **East Province**: 15 km E of Dimako (village halfway Bertoua-Doumé), 11 June 1965, *Leeuwenberg, A.J.M. 5825* (B, BR, C, EA, FHI, GC, K, LISC, MO, P, PRE, SRGH, WAG, YA); S of Elandjo, on km 65 of road Yokadouma-Moloundou, 21 July 1965, *Leeuwenberg, A.J.M. 6227* (BR, K, MO, P, PRE, WAG, YA); Piste Manjoum (feuille Deng-Deng) Gere-feuille IGN 1/200.000 Yoko, 28 June 1959, *Letouzey, R. 2292* (WAG); Forest S of Dimako, bank of river Mobonda, 18 January 1960, *Letouzey, R. 2675* (P, WAG); 3 km of Momjepom (km 22 road Yokadouma-Moloundou, 19 June 1963, *Letouzey, R. 5198* (P, WAG); On 15 km SSE of Yokadouma, 23 March 1973, *Letouzey, R. 12155* (P, WAG); **South-West Province**: around Kupe Mountain, Tombel, Etam Forest Reserve, 20 August 1986, *Etuge, M. 214* (WAG); Bole-Meboka, Kumba-Mamfa road, 4 July 1987, *Thomas, D.W. 7156* (NY);

CENTRAL AFRICAN REPUBLIC: **Lobaye**: Mbaiki and Boukoko region, Boukoko station, 12 June 1950, *Tisserant, C., Equipe 1775* (BM, WAG);

CONGO (KINSHASA): **Bas-Congo**: Lukula, Kondo (station INERA), 26 January 1979, *Breyne, H. 3553* (BR); Lovo, 27 November 1959, *Compère, P. 911* (BR); Mindombela, 18 September 1951, *Devred, R. 683* (BM, BR); Luki, 14 December 1947, *Donis, C. 1634* (BR); M'vuazi, 16 April 1957, *Dubois, J. 181* (BR, WAG); **Equateur**: Libenge, *Gilbert, G. 1833* (BR, P, WAG); Libenge, 21 June 1938, *Leontovitch, C. 78* (BR); **Nord-Kivu**: Kivu Province, River Tungula, 18 September 1952, *Osmaston, H.A. 2642* (BM); **Orientale**: between Dunge and Faradge, *De Schlippe 217* (BR); Bogoro, June 1937, *Gilbert, G. 1595* (BR, G, WAG); Ituri, Epulu area, 19 September 1954, *Gutzwiller, R. 412* (BR); Bambesa, 20 June 1952, *Gérard, P. 199* (BR); Bambesa, 28 September 1953, *Gérard, P. 1036* (BR); Bambesa, 14 May 1957, *Gérard, P. 2856* (BR, MO); Bambesa, 8 May 1957, *Gérard, P. 2886* (BR, WAG); Mambasa (Ituri forest), 29 March 1993, *Hart, T.B. 1525* (BR, MO); Uéle-Kimbiri, Bondo, March 1981, *Lebrun, J. 2425* (BR);

ETHIOPIA: **Illubabor**: 17 km east of Punido, along the new road to Gog, 24 November 1995, *Friis, I. 7319* (C, K); **Kefa**: Kefa A. region: 20 km SW of Aman (Mezan Tefari airstrip), 29 November 1984, *Friis, I. 3865* (C, K); Kefa A. region: Bebeka coffee plantation, S of Mezan Tefari. About 5 km southwest of the coffee plantation, 4 December 1984, *Friis, I. 3991* (C, K);

GHANA: **Unknown**: Kade A.R.S. Arboretum, 28 March 1970, *Hall, J.B. 40153* (GC, MO); Bosomoa Forest Reserve, June 1933, *Vigne, C. FH 3003* (NY);

GUINEA: **Kissidougou**: Kissidougou, 14 April 1949, *Adam, J.G. 4406* (MO);

IVORY COAST: **Abengourou**: Surroundings of Kodjina, 15 km SW of Abengourou, 28 July 1969, *Versteegh, C. 579* (BR, WAG); **Agboville**: Bouroukrou, 92 km on the railroad, 20 December 1906, *Chevalier, A. 16130* (P, WAG); **Bouna**: P.N. Comoé, Kakpin, 14 March 1990, *Chatelain, C. s.n.* (CSRS; not seen!); **Daloa**: F.C. du Haut-Sassandra, Sud. forêt peu dégradée, layon 28, Est CTFT, 19 July 1995, *Kouamé, F.N. 1530* (CSRS; not seen!); **Unknown**: March 1947, *Andoh, J.E. 4976* (MO); SL. relevé 57, 13 November 1992, *Chatelain, C. 1061* (G); Lamto, 21 August 1974, *Devineau, J.-L. 1010* (LAMTO; not seen!); Lamto, 28 June 1989, *Gautier, L.; Béguin, D. 1329* (CSRS, G, LAMTO); Lamto, 12 October 1992, *Tondoh, J. 108* (LAMTO; not seen!); Lamto, *Vuattoux, R. s.n.* (LAMTO; not seen!); **Vavoua**: F.C. du Haut-Sassandra, Centre, forêt peu dégradée, relevé FNK10, 21 June 1994, *Kouamé, F.N. 1293* (CSRS; not seen!); F.C. du Haut-Sassandra, Nord. bord de piste, entre layons 11 & 12, 30 June 1994, *Kouamé, F.N. 1364* (CSRS; not seen!);

NIGERIA: **Edo State**: South Nigeria, Sapoba, *Kennedy, J.D. 1872* (K); Ugo- Urhuehue Motor road, 23 November 1959, *Olorunfemi, J. FHI 43865* (FHI, WAG); Benin Province, 22 March 1935, *Ross, R. 131* (BM); **Osun State**: Ijebu Province, Shasha Forest Reserve, 2 March 1935, *Ross, R. 50* (BM, MO); **Oyo State**: Busogboro village, 10 March 1993, *Daramola, B.O. 53* (K); Ibadan campus University, March 1967, *Gurk, D.P.M. 3138* (IFE, MO);

SUDAN: **Eastern Equatoria**: Equatoria Prov., 9 June 1939, *Andrews, F.W. 1752* (BM, K); Talanga, 26 November 1980, *Friis, I.; Vollesen, K. 479* (C); Talanga, 24 November 1980, *Friis, I.; Vollesen, K. 490* (C); **Western Equatoria**: S.W. Equatoria province, Azza forest, S of Meridi, 16 March 1939, *Hoyle, A.C. 760* (BM, K);

TANZANIA: **Kilimanjaro**: Gonja Forest Reserve, between Mtundu & Mpirani, Villages, 28 February 2001, *Festo, L. 986* (MO); Going Forset Reserve, forest edge at NE boundary of reserve along road from gonja maore to Mpirani, 28 February 2001, *Gereau, R.E. 6628* (MO); **Morogoro**: Morogoro District, Turiani, 3 June 1933, *Burtt, B.D. 4728* (K); Kilosa Disrict, T6, Chunga Wale, 21.2 miles from HQ, 25 June 1973, *Greenway, P.J. 15237* (MO); T6.Udzungwa Mountains National Park. Beside Mwaya River, 4 February 1998, *Massawe, G. 159* (C, MO); Isyaga river, Mahenge, 14 April 1988, *Mhoro, B. 5707* (MO); **Pwani**: T6, Mtemere, along Rufiji, 1 May 1976, *Vollesen, K. 3515* (C); T6 Mtemere, 9 June 1976, *Vollesen, K. MRC 3853* (C, WAG); **Tanga**: Tanga District, 7 miles E of Korogwe. Maguna Estate, on lower slopes of E Usambaras, 26 June 1953, *Drummond, R.B. 3016* (K); Muheze District, Longuza, Forest Project station, 4 July 1977, *Magogo, F.C. 737* (K); Morogoro Golf course, 26 December 1933, *Michelmore, A.P.G. 866* (K);

TOGO: **Unknown**: near Amakpave', *Berg, C.C. 138* (MO); Glei, 20 km S of Atakpamé, 9 December 1977, *Ern, H. 2662* (P, TOGO); Glei, in village, 27 February 1978, *Ern, H. 3226* (B, P, TOGO); Tokpli-village, 25 June 1985, *Schäfer, P.A. 8596* (B, K, LUA, MO, MPU, P, WAG);

UGANDA: January 1916, *Dümmer, R.A. 2788* (K); Budongo, October 1935, *Eggeling, W.J. E 2259* (BM); 9 February 1960, *Letouzey, R. 2973* (P); **Western Province**: Masindi district, Budongo Forest, 29 June 1998, *African tropical Biodiversity Program 702* (MO); Masindi District, Budongo forest, Kaniyo pabidi beat, February 1996, *Hafashimana, D.L.N. 19* (C); N Bunyoro, Bujenje, Royal mile Budongo, 14 August 1977, *Katende, A.B. 2744* (MO); District: Masindi. Budongo Forest Reserve, 20 August 1995, *Nkuutu, D.N. 6- 8* (C); Budongo Forest Reserve, 25 August 1995, *Nkuutu, D.N. 7- 34* (C); District: Bunyoro, Bundongo, 24 September 1962, *Styles, B.T. 64* (BR, FHO); Bundongo, 29 September 1962, *Styles, B.T. 110* (BR, FHO).

Chapter 8

THE "*CELTIS PHILIPPENSIS* COMPLEX"

A. SATTARIAN & J.J. WIERINGA

Summary

Celtis philippensis Blanco was a widespread species with different ecological settings. We found it could be divided into 5 quite distinct morphological groups. Each entity had its own geographical area; in this study we used *ITS* marker, to test *Celtis philippensis* as complex species. We see that 3 of the 4 sampled entities of the complex group together and indeed seem to constitute a complex, with the support for an internal branch in the complex being lower (68%) than that of most other branches outside the complex (82-100%). The support for the complex itself is high (93%). The fourth sampled entity of the complex, *C. malagasica* does not end up with the other members of the complex, and seems to be not related to them. To really address questions on specific delimitation and phylogentic relations within this complex, further sampling, both from more species and from different geographical origin, is urgently needed.

8.1 Introduction

For a review of species, particularly those occurring in Africa, see Chapters 1 and the previous Chapter 7. One species of *Celtis*, *C. philippensis* Blanco, was considered to be particularly widespread, with a distribution from Tropical Africa and Madagascar over India, Burma, SE China, Taiwan, Indo-China, Thailand, throughout Malaysia to NE and West Australia and the Solomon Islands (Soepadmo, 1977). Soepadmo distinguished two varieties, *C. philippensis* var. *philippensis* and *C. philippensis* var. *wightii,* and noted they may not be clearly distinguished. Previous authors such as Polhill (1963) and Letouzey (1972) had considered this entity as a complex, comprising several species, while in reaction on Soepadmo's publication Hewson (1989) remarked that some Australian specimens did not fit in *C. philippensis*.

While going through various herbarium accessions of this *C. philippensis* complex from Africa, Asia, Australia, and Madagascar, we found it could be divided into 5 quite distinct morphological groups. Each entity had its own geographical area; overlap between two entities only occurs in East Africa and Thailand. Now the question arises: are these 5 entities merely geographical forms of a single species, or are they really distinct species.

Based on the morphology of the specimens, we could split up the *Celtis philippensis* complex into *C. philippensis* s.str. restricted to S.E. Asia (Indonesia, Malaysia and Thailand to the Philippines and Taiwan), *Celtis wightii* from Tanzania and Asia (from India to China and Thailand), *C. prantlii* from Africa, *C. madagascariensis* endemic to Madagascar, and *C. australiensis* from Australia (see more details in chapter 4 & 7 in this thesis). The last two entities did not yet have an available name, and, based on the morphological study and the results presented in this chapter, were described as new by Sattarian & van der Maesen (2005). Regrettably the name *C. madagascariensis* proved to be preoccupied, and has to be replaced by *C. malagasica* Sattarian (see above).

To provide a framework for further studies on delimitation and relationships within the *Celtis philippensis* complex we want to add a molecular marker for phylogenetic analyses. To examine the hypothesis of one versus several species within a complex, we have to use a marker with a relatively high substitution rate. The internal transcribed spacer (*ITS*) region nuclear ribosomal DNA is a proven source of useful phylogenetic characters at this taxonomic level (Yesson et al. 2004; Abigail 2003), although it is also known for a whole set of potential problems (Alvarez & Wendel 2003; Wieringa & Gervais 2003).

8.2 Materials and Methods

In molecular systematics, character selection often boils down to choosing the appropriate DNA region for sequencing (Pelser 2003). But, although there is an enormous variation in evolutionary rates among the different regions of the genome (Soltis 1998) it is often difficult to identify the DNA region with the optimal rate for studying the evolutionary history of the group of interest. This is especially because rates of evolution for any specific DNA region may vary among, or even within, groups (Savolainen et al. 2000). The internal transcribed spacer (*ITS*) region of nuclear ribosomal DNA has been widely used for phylogenetic reconstruction at the level of species (cf. Baldwin 1992) and populations (Chiang & Schaal 1999). Owing to in general high substitution rates, the interspecific and intraspecific variability of the *ITS* provides sufficient phylogenetic information on closely related taxa (Paul et al. 2005; Abigail et al. 2003; Alexandra 2004; Baldwin et al. 1995).

8.2.1 Taxon Sampling

We sampled 4 herbarium specimen of the *Celtis philippensis* complex (table 8.1). Although 4 samples are far too limited to really assess infra-complex relationships, at least these 4 samples represent the 4 main areas where the complex occurs: Africa, Madagascar, Asia and Australia. GenBank accessions of 3 more species of *Celtis* and of *Ulmus, Zelkova* and *Hemiptelea* were added as outgroups.

Table 8.1 Collection data of samples used in this study.

Species	**Family**	**Collector**	**Genbank no.**	**Herbarium**	**Origin**
C. australiensis	Celtidaceae	S.J.Forbes 389	To be added	L	Australia
C. malagasica	Celtidaceae	Linda 436A	To be added	WAG	Madagascar
C. wightii	Celtidaceae	I.Friis 479	To be added	C	Tanzania
C. philippensis s.s.	Celtidaceae	E.F.de Vogel 5874	To be added	L	Indonesia
Zelkova sicula	Ulmaceae		AJ622884	GenBank	Asia
Z. schneiderii	Ulmaceae		AJ22876	GenBank	Asia
Ulmus minor	Ulmaceae		AJ622836	GenBank	Asia
Hemiptelea davidi	Ulmaceae		AJ622832	GenBank	Asia
C. africana	Celtidaceae		AJ630212	GenBank	Africa
C. australis	Celtidaceae		AJ630210	GenBank	Asia
C. tournefortii	Celtidaceae		AJ580069	GenBank	Asia

Total genomic DNA was extracted from herbarium or silica-dried leaves (10-25 mg) using the modified CTAB extraction protocol of Doyle (1987), following the DNA extraction protocol of the Biosystematics Group (Vrielink et al. 2005 and chapter 3). Internal transcribed spacer (*ITS*) regions were PCR amplified and sequenced (White et al. 1990).

8.2.2 Phylogenetic analyses

Sequences were assembled and edited using the Staden version 1.5.3, (http://Staden. Sourceforge.net/) alignment of sequences was carried out using Bio-Edit (Hall 1999), more alignments were done by eye using the same software (see Sattarian et al. 2006, chapter 3), and MacClade version 4.07 (PPC). Indels in alignments were coded as present/absent characters where they could be coded unambiguously, following the simple indel coding protocol as described by Simmons (2000).

Data were analyzed using the parsimony algorithm of the software package PAUP version 4.0b10 for Macintosh (PPC), on a Macintosh G5. Subsequently a jackknife analysis was performed. We used jackknife support analysis with heuristic search, number of jackknife replicates 1000, nominal percentage of characters deleted in each replicates 37, 1248 characters, all the characters are of unordered type, all characters have equal weight. Gaps were treated as missing, addition sequence was random. Number of replicates 10, number of trees held at each step during stepwise addition 1, Branch-swapping algorithm tree-bisection-reconnection (TBR).

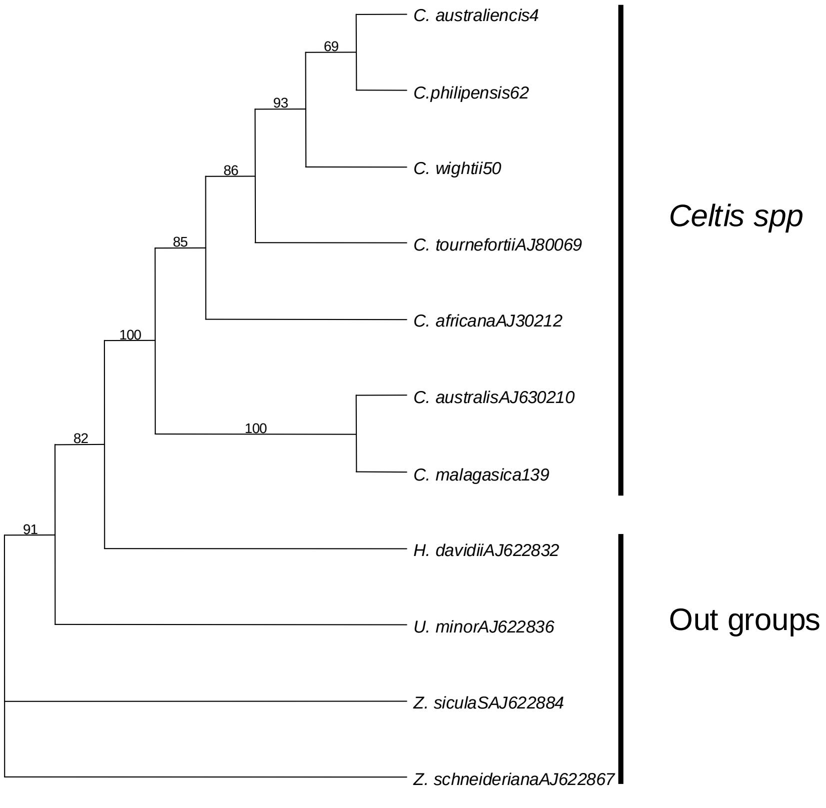


Figure 8.1. MP majority-rule consensus cladogram (1000 replicates, TBR swapping). Support values > 50 % are shown (*ITS* marker).

8.3 Results and discussion

In this study for analysis we used maximum parsimony.The *ITS* region has an aligned length of 721 characters, (*ITS*, indel) and contains 162 parsimony informative characters (22.4%). The Mp resulted in a single tree of 566 steps, CI = 0.725, RI = 0.858 (Fig. 8.1), the majority rule consensus tree based on *ITS* and indel has 8 nodes.

The topology of the Jackknife analysis shows a *Celtis* clade with 100% support. The number of the *Celtis* species included here is very low, and taxon sampling here for aims of phylogeny is very poor but in the clade of the *Celtis*, *Celtis australiensis* from Australia and *Celtis philippensis* from South Asia are sister groups with 69% support, and sister to *C. wightii* from Africa with 93% support. These in their turn are sister to the Asian *Celtis tournefortii* with 86% support, with the next joining species being African again: *Celtis africana*. This entire clade is sister to a clade containing the other 2 species in this analysis: *C. australis* and *C. malagasica.*

We see that 3 of the 4 sampled entities of the complex group together and indeed seem to constitute a complex, with the support for an internal branch in the complex being lower (68%) than that of most other branches outside the complex (82-100%). The support for the complex itself is high (93%). The fourth sampled entity of the complex, *C. malagasica* does not end up with the other members of the complex, and seems to be not related to them at all. This topology renders it even more surprising they were ever confused at all; this is reflected in the morphology as well, with the morphological differences with for instance *C. prantlii* and *C. philippensis* being quite striking. The fifth entity of the complex, *C. prantlii,* is not included in this study, and should be added to see if it is part of the real complex, or that it falls outside alike *C. malagasica*. Our morphological study, however, indicates it *C. prantlii* is closely related to *C. wightii,* so most likely it will belong to the complex. More material, especially of African *C. wightii* specimens, is needed to assess whether this Tanzanian population really is conspecific with Asian *C. wightii*, or that it may belong to *C. prantlii*. More molecular data will be most useful.

To really address questions on specific delimitation and phylogentic relations within this complex, further sampling, both from more species and from different geographical origin, is urgently needed. *ITS* nowadays is often considered a problematic marker, presenting problems like paralogs (see Alvarez & Wendel 2003). Although in this study so far no length variation within a sample was detected, it might be useful to consider other markers, or even other techniques, i.e. AFLP’s™, to further assess this complex.

Chapter 9

CONSPECTUS OF *CELTIS* (CELTIDACEAE) SPECIES WORLDWIDE

A. SATTARIAN & L. J. G. VAN DER MAESEN

Introduction

An attempt was made to provide basic information about all names produced in *Celtis* in the course of taxonomic history. The protologues were obtained to procure details of the type and its whereabouts. Information from databases such as the International Plant Names Index was completed from various sources. The present geography was gleaned from Flora's and some more recent literature e.g. Berg & Dahlberg (2001). The status of many names is unsure, as this thesis is focused on African species, and this conspectus should be considered as a first step to oversee all *Celtis* species and the formidable synonymy in cases. Hence no decision was made on synonymy, and we merely followed the opinion of Flora's and regional revisions as far as most non-African species are concerned. Not all literature was available. Most species are small or larger trees, and descriptive elements were omitted.

***Celtis acata* Buch.-Ham.**, Trans. Linn. Soc. 17: 211 (1834).
Type: India: near Gongachor, Hamilton. K, L. Syn. of *C. australis* L. India.
***Celtis aculeata* Sw. var. *aculeata*,** Nov. Gen. Sp. Pl. Prodr. 53 (1788).
Type: Ind. Occid., Swartz s.n. Holotype: S; iso: B, K, IEI. Syn. of *C. iguanaea* (Jacq.) Sarg. Basionym: *Mertensia aculeata* (Sw.) Schult., *Momisia aculeata* (SW.) Klotzsch; *Ziziphus commutata* (as *commutatus*), apparently to substitute the name *Celtis aculeata*, *Mertensia commutata* (Roem. & Schult.) Hemsl. South America: Dominican Republic, Cuba, Mexico, Venezuela, Granada, Peru.
***Celtis aculeata* Sw. var. *laevigata* (Kunth) Planch.**, in DC. Prodr. 17: 187 (1873).
Type: Mexico. Campeche: without locality, Humboldt s.n. Holotype: B or P. Syn. of *C. iguanaea* (Jacq.) Sarg.
***Celtis aculeata* Sw. var. *pubescens* Griseb.**, Fl. Br. W. Ind. Isl. 149 (1859).
Type: Jamaica. 25 July 1850, Alexander Prior s.n. 291. Holotype: GOET; iso: K. Syn. of *C. iguanaea* (Jacq.) Sarg.
***Celtis aculeata* Sw. var. *serrata* Griseb.**, Fl. Br. W. Ind. Isl. 149 (1859).
Type: Jamaica. Mar. 1856 (?), Macfayden s.n. Holotype: GOET; iso: K. Syn. of *C. iguanaea* (Jacq.) Sarg.
***Celtis adolfi-friderici* Engl.**, Bot. Jahrb. Syst. 43: 308 (1909).
Type: Congo Dem. Republic, Kivu Province, few km W of foot of Mt. Ruwenzori: Mildbread 2725; in Kwa Muera forest NW of Beni: Mildbread 2169; in Kwa Muera forest NW of Beni: Mildbread 2242 Syntypes: B. Accepted. E. Africa, Uganda, Sudan, Congo Republic,Botswana, Zambia, Mozambique, Malawi, Zimbabwe.
***Celtis affinis* De Wild.**, Rev. Zool. Afr. 9 Suppl. Bot. B1. (1921).
Type: Congo Dem. Republic, Bequaert 3301, 3259. Syntypes: BR. Syn. of *C. zenkeri* Engl. Africa.
***Celtis africana* Burm.f.**, Fl. Cap. Prodr. 31 (1768).
Type: Africa: Burmann. K, BM. Accepted. Syn.: *Celtis kraussiana* Bernh. Eritrea, Somalia, Ghana, Nigeria, Cameroon, Central African Republic, RD Congo, Ethiopia, Uganda, Kenya, Tanzania, Angola, Zambia, Malawi, Mozambique, Swaziland, Lesotho, Yemen.
***Celtis alba* Rafin.**, Fl. Ludov. 25 (1871).
Type:. Accepted. North America.
***Celtis albicans* Willd. ex Steud.**, Nom. Ed. 2. 1. 316 (1840).
Type: Syn. of *Trema micrantha* Sw., *Sponia canescens*.
***Celtis alnifolia* (Wedd.) Miq.**, Mart. Fl. Bras. 15 (1): 175 (1853).
Type: Brazil: prov. Mato Grosso, forest of junction of Cuxipo river, Weddell 3028. Holotype: P, iso: P, photograph in G. Syn. of *C. iguanaea* (Jacq.) Sarg. Tropical America.

***Celtis alpina* Royle**, Illustr. Bot. Himal. 341 (1835/39).
Type: India. B, BM, K, G, BM, CGE, K.
***Celtis amblyphylla* F.Muell.**, Fragm. 9: 76 (1875).
Type: Australia: Howe Island, Moore & Fullagar s.n. Holotype: MEL; iso: K. Basionym of *C. conferta* Planch. subsp. *amblyphylla* (F.Muell.) P.S.Green. Australia.
***Celtis amboinensis* Buch.-Ham. ex Wall.**, Wall. Cat. n. 3693 (1831).
Type: Nomen. K-Wall. Syn. of *Trema politoria*.
***Celtis amboinensis* Willd.**, Sp. Pl. ed. 4: 997 (1806).
Type: Syn. of *Trema amboinensis* (Willd.) Blume.
***Celtis americana* Mill.**, Gard. Dict. ed. 7. n. 4 (1768).
Type: Accepted. N. America.
***Celtis americana* Hort. ex Planch.**, in DC. Prodr. 17: 176. 1873.
Type: Hort. Paris., herb. Thouin, Cambessedes. Holotype: P, iso: MPU? Syn. of *C. mississipiensis* Bosc.
***Celtis amphibola* C.K.Schneid.**, Sarg. Pl. Wils. 3. 279 (1916).
Type: China:Yunnan, Mengtsze, Henry 9323. A, B, E, HK. Accepted. China.
***Celtis amplifolia* Noronha**, Verh. batav. 5. ed. 1. Art. 4. 11 (1790).
***Celtis anfractuosa* Liebm.**, Vidensk. Selsk. Naturvidensk. Math. Afh., Ser. 5, 2: 338. (1851).
Type: Mexico: Veracruz: Xalcomulco (=Jalcomulco) Jul. 1841, Liebmann 5894. Holotype: C. Syn. of *C. iguanaea* (Jacq.) Sarg.
***Celtis angustifolia* Lindl.**, Wall. Cat. n. 3691(1831).
Type: India, Wallich. K-Wall, U. Syn. of *Trema angustifolia*.
***Celtis angustifolia* (Miq.) Planch.**, in DC. Prodr. 17: 186 (1873).
Basionym: *Solenostigma angustifolium* Miq. Type: W. Sumatra. Holotype: U. Syn. of *Ziziphus angustifolia*(Miq.) Hatus. ex Steenis. India, Burma, Thailand, Sumatra, Malaysia, Philippines, New Guinea.
***Celtis aphanonthoides* Koidz.**, Bot. Mag. Tokyo 27: 563 (1913).
Type: Japan. Syn. of *C. jessoensis* Koidz. Japan.
***Celtis appendiculata* E.Mey. ex Planch.**, Ann. Sc. Nat. Bot. sér. 3, 10: 341 (1848).
Type: South Africa, distr. Uitenhage, Galgebosch, in forest, Drège s.n. Holotype: P; iso: K. Syn. of *Chaetachme aristata* Planch.
***Celtis arcata* Buch-Ham. ex Wall.**, Wall. Cat. n. 3695 (1831).
Based on India, Gungachora, Parroma & Sukanaghur, Hamilton. K-Wall. Syn. of *C. australis* L.
***Celtis aristata* E.Mey. ex Planch.**, Ann. Sc. Nat. Bot. sér. 3, 10: 341 (1848).
Type: S. Africa, Osawumbo, below 1000 ft., Drège s.n. Holotype: P; iso: K. Syn. of *Chaetachme aristata* Planch.
***Celtis aspera* Brongn.**, Duperr. Bot. Voy. Coq. 213. t. 48 (1829).
Type: Australia: Blue Mountains, near Port Jackson, Lesson d'Urville. Syn. of *Trema aspera*.
***Celtis aspera* Lodd. ex G. Don**, in Loudon, Hort. Brit. 413 (1830).
Type: nom. in synonymy of *C. occidentalis*. N. a. Syn. of *C. australis* L.
***Celtis asperifolia* Merr.**, Philipp. J. Sci. 17: 246 (1920).
Type: Philippines: Mindanao, Davo prov. Santa Cruz: For. Bur. 27562 De Mesa. Holotype: PNH; iso: Syn. of *C. rigescens*. Mindanao.
***Celtis asperrima* Lojac.**, Fl. Sci. 2, 2: 355 (1907).
Type: Brazil, Para: Without locality, Martius s.n. Holotype: M, Photographs in MO and NY; Isotype (fragment): U.
***Celtis asperula* Miq.**, in Mart. Fl. Bras. 4, 1. 176 (1853).
Type: Brazil: Para, no locality, Martius s.n. Holotype: M., Photograph in MO and NY; Isotype (fragment); U. Syn. of *C. iguanaea* (Jacq) Sarg. America, Mexico, Guatemala, El salvador, Nicaragua, Panama, Peru, Ecuador.
***Celtis audibertiana* Spach var. *audibertiana*,** Ann. Sc. Nat. Paris Sér. 2, 16: 41 (1841).
Type: N. America. P. Accepted.
***Celtis audibertiana* Spach var. *oblongata* Spach**, Ann. Sc. Nat. Paris Sér. 2, 16: 41 (1841).
Type: N. America. P. Accepted.
***Celtis audibertiana* Spach var. *ovata* Spach**, Ann. Sc. Nat. Paris Sér. 2, 16: 41 (1841).
Type: N. America. P. Accepted.
***Celtis aurantiaca* Nakai**, Chosen Sanrin Kwaiho 59: 23 (1930); Fl. Sylvat. Koreana 1: 63 (1932).
Type:. Accepted. Korea, N.E. China.
***Celtis australiensis* Sattarian**, Blumea 50: 499 (2005).
Type: W. Australia: Dampier distr., Geikie Gorge, Telford 11722. Holotype: CBG; iso: BISH, BRI, L, NSW, PERTH. Accepted. Australia, WA, NT, Qld.
***Celtis australis* A.Rich.**, Tent. Fl. Abyss. 2: 257 (1851).
Type: Syn. of *C. kraussiana* Bernh., hence *C. africana* Burm.f.

Celtis australis **L.**, Sp. Pl. 1043 (1753).
Type: Habitat in Europae australi & Africa citeriore. Herb. Linn. 1209.2. Lecto: LINN. Accepted. S. Europe, Afghanistan, N.W.India (Himalaya), C. Asia, N. Africa. Widely introduced.
Celtis australis **L. subsp. *caucasica* (Willd.) C.C.Townsend**, Fl. Iraq 4, 1: 73 (1980).
Basionym: *C. caucasica* Willd. Iraq, Turkey, Iran, W. Pakistan, Afghanistan, N.W. India, C. Asia, S. Europe.
Celtis azcurrensis **Parodi**, Anal. Soc. cient. Argent. 5: 152 (1878).
Type: Paraguay: Asunción, Anon. s.n. Argentina. Not traced (Berg & Dahlberg 2001). Possibly *Celtis ehrenbergiana*.
Celtis bainingensis **Rech.**, Denkschr. Akad. Wiss. Wien 532 (1914).
Celtis balansae **Planch.**, in DC. Prodr. 17: 183 (1873).
Type: New Caledonia, Bourail, on the Nera river, Balansa 1041. Holotype: P.
Celtis bequaerti **De Wild.**, Rev. Zool. Afr. 9. Suppl. Bor. 2 (1921).
Type: RD Congo. BR. Syn. of *C. mildbraedii*.
Celtis berlandieri **Klotzsch**, Linnaea 20: 541 (1848).
Type: Mexico. A, B, BM, BP, F, FI, G, MO, NY. Syn. of *C. laevigata*
Celtis berteroana **Urb.**, Rep. Sp. Nov. Regni Veget. 15: 109 (1917).
Type: Jamaica, Bertero 2116, Fuertes 670. Jamaica.
Celtis betulaefolia **Vandas**, Oest. Bot. Zeitschr 39: 221 (1889).
Type: Herzegowina, B, A, BH, L, SI.
Celtis betulina **Lojac.**, Fl. Sci. 2 (2): 355 (1907).
Type: Sicily.
Celtis bifida **Leroy**, Bull. Soc. Bot. France 95: 7 (1948).
Type: Madagascar, vallee du Fiherama, Grève 212. Holotype: P. Accepted.
Celtis biflora **Ruiz. ex Miq.**, Mart. Fl. Bras. 4. (1). 182 (1853).
Type: Peru and New Grenada.
Celtis biflora **Ruiz & Pav.**
Celtis biondii **Pamp.**, Nuov. Giorn. Ital. 17: 252 (1910); Bull. Soc. Tosc. Ortic. ser. 3: 214 (1911).
Type: China, Kouy-Tcheou, environs de Koug-yang, bois de la Pagoda Longo-chan A, P, LU, LI. Accepted. C. China, Japan, Taiwan.
Celtis biondii **Pamp. var. *biondii*,** Bull. Soc. Tosc. Ortic. ser. 3: 214 (1911).
Type: China: Hupeh.
Celtis biondii **Pamp. var. *cavalieri* Schneid.** W. China
Celtis biondii **Pamp. var. *heterophylla (Lév.)* Schneid.** Korean Peninsula.
Celtis biondii **Pamp. var. *holophylla* (Nakai) E.W. Ma**, Bull. Lab. North-East. Inst. 7: 125 (1980).
Type: Syn.: *C. leveillei* var. *holophylla* Lév.
Celtis biondii **Pamp. var. *insularis* Hatusima**, Fl. Ryukyus 224 (1971), no latin descr.
Type: Japan, Ryukyu Isl.
Celtis bodinieri **Leveillé**, Feddes Repert. 13: 265 (1914).
Type: China, Yunnan: Kouy-Tcheou, Environs de Kouy-yang. A, P, NTM.
Celtis boliviensis **Planch.**, Ann. Sc. Nat. Bot. Sér. 3, 10: 311 (1848).
Type: Bolivia. Without locality, 1839, Pentland 72. Holotype: K; iso: P. Syn. of *C. brasiliensis* (Gardner) Planch.
Celtis boninensis **Koidz.**, Bot. Mag. Tokyo 27: 183 (1913).
Type: Japan. Kuwanoha-yenoki. Syn. *Celtis jessoensis* Koidz. Japan, Bonin. Liukiu, insl. Okinawa.
Celtis bonplandiana **Planch.**, in DC. Prodr. DC. 17: 190 (1873).
Type: Argentina. Corrientes: without locality, Bonpland 943. Holotype: P. Syn. of *C. ehrenbergiana* (Klotsch) Liebm.
Celtis brasiliensis **(Gardner) Planch.**, Ann. Sci. Nat. Bot. sér. 3, 10: 310 (1848).
Type: Brazil, Rio de Janeiro: Serra dos Orgao's, Mar 1873, Gardner 347. Holotype: K, A, B, BM, BR, CN, DR, E, F, FI. Accepted. Basionym: *Mertensia brasiliensis* Gardner, London J. Bot. 2: 3391(843).
Celtis brasiliensis **(Gardner) Planch. f. *clausseniana* (Wedd.) Planch.**, in DC. Prodr. 17: 189 (1873).
Type: Brazil.Minas Gerais: without locality, 1838, Claussen 1067. Holotype: P; iso: P.
Celtis brevifolia **(Klotzsch) Miq.**, in Mart., Fl. Bras. 4, 1: 180 (1853).
Type: South America (Guayaquil?) Ruiz s.n. Holotype: B. Syn. of *C. iguanaea* (Jacq.) Sarg. Basionym: *Momisia brevifolia* Klotzsch, Linnaea 20: 5381(847).
Celtis brevinervis **(Blume) Planch.**, in DC. Prodr. 17: 183 (1873). Basionym: *Solenostigma brevinerve* Blume, Mus. Bot. Lugd. Bat. 2: 67 (1856). Type: New Guinea, Zippel Holotype: L. Syn. of *C. paniculata*.
Celtis brevipes **S.Watson**, Proc. Am. Acad. 14. 297 (1879).
Celtis brieyi **De Wild.**, Miss. de Briey Mayumbe 11: 1 (1920).
Type: DR Congo: Region of Ganda-Sundi, Count J. de Briey 152. Holotype: BR. Syn. of *C. tessmannii* Rendle. West Trop. Africa.
Celtis brownii **Rendle**, Journ. Bot. 53. 298 (1915).
Type: Uganda, Mabira forest, E. Brown 462. Lectotype: BM; iso: K. Syn. of *C. prantlii* Priemer ex Engl.

Celtis bungeana **Blume**, Mus. Bot. Lugd. Bat. 2: 71 (1856).
Type: China, Japan. GH, SU. Accepted. Central and North Asia.
Celtis bungeana **Blume var. *bungeana*,** Mus. Bot. Lugd. Bat. 2: 71 (1856).
Celtis bungeana **Blume var. *heterophylla* Lév.**
Type:. Syn. of *C. biondii* var. *heterophylla*
Celtis bungeana **Blume var. *jessoensis* (Koidz.) Kudo**.
Type: Basionym of *C. jessoensis* Koidz.
Celtis bungeana **Blume var. *deqinensis* Xiang, W.Li & G.S.Fan**, Acta. Bot. Yunnanica 20, 2: 160 (1998), as "*deqiensis*".
Type: Holotype: KUN.
Celtis bungeana **Blume var. *lanceolata* E.W.Ma**, Bull. Bot. Lab. North-East Forest. Inst. 7: 125 (1980).
Celtis burmannii **Planch.**, Ann. Sc. Nat., sér. 3, 10: 296 (1848).
Type: South Africa, Drège s.n. Lectotype: P; isolecotype: K.
Celtis canescens **Kunth**, Nov. Gen. et Sp. 2: 28 (1817).
Syn. of *Trema micrantha*(L.) Blume.
Celtis canina **Raf.**, Am. Monthly Mag. 2: 43 (1817).
Type: Basionym of *Celtis occidentalis* var. *canina*.
Celtis caucasica **Hohen. ex Planch.**, Ann. Sc. Nat. sér. 3. 10: 285 (1848).
Name in synonymy. Syn. of *Celtis australis* L.
Celtis caucasica **Willd.**, Sp. Pl. ed. 4: 994 (1806).
Type: Caucasus on Caspian Sea, Adam 18981. Holotype: B. Var. of *Celtis australis* L. Iran, Afghanistan, Central Asia, Nepal, Kashmir. Sometimes accepted as separate species.
Celtis caucasica **Willd. subsp. *caudata* (Planch.) I.A.Grudz.**, Novosti Sist. Vyssh. Rast. 16: 93 (1979). Basionym *C. caudata* Planch.
Celtis caudata **Hance**, Ann. Sc. Nat. Bot. sér. 5, 5: 241 (1866).
Type: Taiwan, near Tam-sui. Holotype: P. Syn. of *Prunus pogonostyla* Maxim.
Celtis caudata **Planch.**, Ann. Sc. Nat. Bot. sér. 3, 10: 294 (1848).
Type: Mexico, Zimapan, Coulter 1492, commun. Harwey. Holotype: K.
Celtis caudata **Wall. ex Planch.**, in DC. Prodr. 17: 199 (1873).
Type: India, Hogla hill, Wallich 1860. Holotype: P, Herb. DC.
Celtis cavaleriei **Leveille**, Feddes Repert. 1: 440 (1912).
Type: China, Kouy-Tchéou, Pin-Fa, 4 sept. 1902 (Jul. Gavalerie, 349). A, G, K, L, P. China.
Celtis cerasifera **C.K.Schneid.** , Sarg. Pl. Wils. 3: 271 (1916).
Type: China (Hupeh), Collector, Fang Hsein, October 1907.no 593, type, Wushan hsein, September 1907. 442. A, B, DS, E, GH, K, MO, N, NY. Western Hupeh (China).
Celtis cercidifolia **C.K.Schneid.** , Sarg. Pl. Wils. 3: 271 (1916).
Type: China, Western Hupeh, Collector: A. Henry 2262. A, B, BM, BRSL, CAL, DBN, E, F, G, K, L. Syn.: *Celtis sinensis* Hemsley in Jour. Linn. Soc. 26: 450 (non Pers.) (1894). China, Western Tienmushan, In forests, alt. 7000 m.
Celtis chekiangensis **Cheng**, Contrib. Biol. Lab. Sc. Soc. China, Bot. ser. 1: 245 (1934).
Type: Yutsing, western Tienmushan, W.C.Cheng (China)2169. A, BM, DS, E, US. China, Yutsing, Western Tienmushan, alt 7000 m.
Celtis chichape **(Wedd.) Miq.**, in Martius, Flora Bras. 4, 1: 181 (1853).
Type: Bolivia. Santa Cruz: Santa Cruz de la Sierra (Prov.Cordillera),Nov 1845, Weddell 3610. Holotype: P; iso: P, MPU, Photograph in MO. Accepted. Basionym: *Momisia chichape* Wedd., Ann. Sci. Nat. Bot., Sér 3, 18: 193 (1852).
Celtis chichilea **Ruiz & Pav. ex Planch.**, Ann. Sc. Nat. Bot. sér. 3, 10: 335 (1848).
Type: Peru, Collector: Mathews 2038. Tex, Astc. Syn. of *Trema micrantha*. Peru.
Celtis chicopa **Miq.**, in Martius Fl. Bras. 4, 1: 181 (1853).
Type: Syn. of *Celtis chicape* (Wedd.) Miq.
Celtis chinensis **Bunge**, Enum. Pl. Chin. Bor. 61 (1831).
Type: China. China.
Celtis choseniana **Nakai**, Chosen Sanrin Kwaiho, No, 59, 21 (1930); Nakai, Fl. Sylvat. Koreana, 19. 59 (1932).
Type: Korea. TI, A. Syn. *Celtis koraiensis* var. *holophylla* Nakai in Tokyo Bot.Mag. 40: 167 (1956). China, Korea.
Celtis chuanchowensis **Metcalf**, Sunyatsenia, 3, 113 (1936).
Type: China (Fokien), Collector: H.H. Chung 3148, Type, Amoy university, duplicate type, Lingnan Natural History Survey and Museum. A, AU, B, BM, F, FCU, FH. Fukien, Chuanchow, roadside.
Celtis cinerea **Torr.**, Bot. Mex. Bound. t. 50 (year).
Type: Syn. of *Celtis tala*.
Celtis cinnamomea **Lindl.**, Wall. Cat. 130. n. 3696 (1831).
Type: Bangladesh, Sylhet, Wallich no 3696m. India, Assam, Griffith in herb. Hook et Leman. Syntypes: K-Wall., E. In open forest at low altitudes. India and Ceylon to Java and Sumatra, China, Philippines.

***Celtis cinnamomea* Lindl. ex Planch.**, Ann. Sci. Nat. Bot. sér. 3, 10: 303 (1848).
Type: Bangladesh, Sylhet. E. Syn. of *C. timorensis* Span. Himalaya (Nepal, Sikkim), India, Bangladesh, Sri Lanka, Burma, Indo-China, Malaysia.
***Celtis clausseniana* (Wedd.) Miq.**, in Martius, Fl. Bras. 4, 1: 178. (1853).
Type: Brazil: Minais Gerais, no locality, 1838, Claussen 1067. Holotype: P; isotype P. Syn. of *C. brasiliensis* (Gardner) Planch. Other syn.: *Momisia clausseniana* Wedd. *C. chichape* Wedd.
***Celtis collinsae* Craib**, Kew Bull. 370 (1918).
Type: Sriracha, Mrs D. J. Collins, 230,241. A, BM, K, MO, NY, US. Syn. of *C. philippensis* Blanco.
***Celtis commersonii* A.Brong.**, Duperr. Voy. Coq. bot. 215 (±1834).
Type: Syn. of *Trema orientalis*.
***Celtis compressa* A.Chev.**, Bull. Soc. Bot. Fr. 61, Mém. 8: 298 (1917).
Type: Ivory Coast: Bouroukrou, railroad km 92, 20 Dec. 1906 - 20 Jan. 1907, Chevalier 22451, 22460. Syntypes: P. Syn. of *C. mildbraedii*.
***Celtis conferta* Planch.**, in DC. Prodr. 17: 183 (1873).
Type: not given; see vars. *cuneata* Planch. and *elliptica* Planch.
***Celtis conferta* Planch. subsp. *amblyphylla* (F.Mueller) P.S.Green**, J. Arn. Arbor. 67, 1: 120 (1986).
Type: basionym: *C. amblyphylla* F. Muell.
***Celtis conferta* Planch. var. *cuneata* Planch.**, in DC. Prodr. 17: 1911 (1873).
Type: New Caledonia: on the seacoast, Pancher, and Port de France, Vieillard 315. Syntypes: P. Syn. of *C. conferta* Planch.
***Celtis conferta* Planch. var. *elliptica* Planch.**, in DC. Prodr. 17: 1911 (1873).
Type: New Caledonia: Noumea, Balansa 962. Holotype: P. Syn. of *C. conferta* Planch.
***Celtis cordata* Pers.**, Syn. 1: 222 (1805).
***Celtis cordifolia* L'Herit. ex Duham.**, Arb. ed. Nov. 2. 37 (±1835).
Type: Korea. TI. Japan, Chojusan prov. Kokai.
***Celtis cordifolia* Nakai**, Bot. Mag. Tokyo 15: 168 (1926).
***Celtis crassifolia* Lam.**, Encyc. Méth. Bot. 4: 138 (1797).
Type: N. America. P. Syn. of *C. occidentalis* L. var. *cordata*.
***Celtis crassifolia* Lam. var. *crassifolia*,** Ann. Sci. Nat. (Paris) (sér. 2) Bot. 16: 40 (1841).
Type: Not indicated. P.
***Celtis crassifolia* Lam. var. *eucalyptifolia* Spach**, Ann. Sci. Nat. (Paris) (sér. 2) Bot. 16: 39 (1841).
Type: Not indicated. P.
***Celtis crassifolia* Lam. var. *morifolia* Spach**, Ann. Sci. Nat. (Paris) (sér. 2) Bot. 16: 39. (1841).
Type: Not indicated. P.
***Celtis crassifolia* Lam. var. *tiliaefolia* Spach**, Ann. Sci. Nat. (Paris) (sér. 2) Bot. 16: 39 (1841).
Type: Not indicated. P.
***Celtis crenata* (Wedd.) Miq.**, in Mart. Fl. Bras. 4, 1: 181 (1853).
Type: Bolivia: Santa Cruz: Santa Cruz de la Sierra, Prov.Cordillera, Nov. 1845, Weddell 3579. Holotype: P; iso: P. Syn. *of C. brasiliensis* (Gardner) Planch. Other syn.: *Momisia crenata* Wedd., Ann. Sci. Nat. Bot., sér. 3, 18: 195 (1852).
***Celtis crenata* A.Chev.**, Expl. Bot. Afr. Occ. Franc. 1. 588 (1920).
Type: Ivory Coast: Morénou, between Yaboisso and Daoukrou, 4 Dec. 1909, Chevalier 22488 & Benin: near Zagnanado, between Abbo and Massé, 6 Feb. 1910, Chevalier 22575. P. Syn. of *C. prantlii* Priemer ex Engl.
***Celtis crenata* Miq.**, in Mart. Fl. Bras. 4 (1). 181 (1853).
Type: Bolivia: Santa Cruz: Santa Cruz de la Sierra (Prov. Cordillera) Nov. 1845, Weddell 3579. Holotype: P, iso: P. Syn. of *C. tala*. In prov. S. Cruz de la Sierra Boliviae.
***Celtis crenata* Planch.**, in DC. Prodr. 17: 1911 (1873).
Type: Bolivia: Prov.Cordillera, Santa Cruz de la Sierra, Nov.1845, Weddell 3579. Holotype: P; iso: P.
***Celtis crenato-serrata* Merr.**, Philipp. J. Sci. 5. 174 (1910).
Type: Philippines, Luzon, Province of Bataan, Duale, Forest Bur. 20043 Tapacio, 2 Oct. 1909. BR. Luzon, Province of Bataan, Duale,
***Celtis curiandiuba* Gomez ex Planch.**, in DC. Prodr. 17: 204 (1873).
Type: SI, LIL. Syn.: *Trema micrantha*.
***Celtis davidiana* Carr**, Rev. Hortic. 300 (1868).
Type: China. P. Syn. of *C. bungeana*.
***Celtis dichotoma* (Klotzsch) Ruiz ex Miq.**, in Mart. Fl. Bras. 4, 1: 182. (1853).
Type: Peru: Pasco: Pozuzo, Chacahuassi, Ruiz & Pavon s.n. Holotype: B; iso: B. Syn. of *C. iguanaea* (Jacq.) Sarg.; Basionym: *Momisia dichotoma* Klotzsch, Linnaea 20: 539.1847.
***Celtis dichotoma* Ruiz ex Miq.**, in Mart. Fl. Bras. 4, 1: 182. (1853).
Type: Peru. Holotype: B; iso: B.

Celtis diffusa **Planch.**, Ann. Sci. Nat. Bot. sér. 3, 10: 314 (1848).
Type: Brazil: Arraial das Merces, Oct 1840, Gardner 5184. Holotype: K. Syn. of *C. iguanaea* (Jacq.) Sarg. Brasiliae prov. Minas Geraes, loco dicto Arraial das Merces.
Celtis dioica **S.Moore**, Bot. J. Linn. Soc. 11: 204 (1911).
Type: Zimbabwe: Gazaland, Chirinda Forest, Swynnerton 108. Holotype: K; iso: BM. Syn. of *C. gomphophylla* Baker. Chirinda forest, 3700-4000 ft.
Celtis discolor **A.Brongn.**, Duperr. Voy. Coq. Bot. 1: 215. t. 47. f. B. (±1834).
Type: Basionym of of *Trema discolor* Blume.
Celtis disticha **Parodi**, Anal. Soc. Cient. Argent. 5: 96 (1878).
Type: Paraguay: Caaguazú, Apr. 1863, Anon. s.n. Not traced. Possibly not *Celtis.*
Celtis djungiel **(Blume) Planch.**, in DC. Prodr. 17: 185 (1873).
Type: Indonesia: W. Java. U. Basionym *Solenostigma djungiel* Blume. Syn. of *C. philippensis* Blanco.
Celtis douglasii **Planch.**, Ann. Sc. Nat. sér. 3. 10: 293. (1848).
Type: Canada: British Colombia, Douglas s.n. Herb. Hook., Herb. Lindl. Accepted. Canada, USA.
Celtis dubia **De Wild.**, Rev. Zool. Afr. 9. Suppl. Bot. 5 (1921).
Type: DR Congo: Bequaert 2525 (holotype: BR);. Holotype: BR. Syn. of *C. mildbraedii*.
Celtis dumosa **Casar. ex Planch.**, in DC. Prodr. 17: 188 (1873).
In synonymy of *C. ferruginea* (Wedd.) Planch..
Celtis durandii **Engl.**, Notizbl. Bot. Gart. Berlin, 3. 222 (1900).
Type: Congo, Tanzania, Trotha 171. B, BR, L. Syn. of *C. gomphophylla* Baker. Uganda, Kenya, Tanganyika.
Celtis durandii **Engl. var. *ugandensis* (Rendle) Rendle**, Fl. Trop. Afr. 6, 2: 5 (1916).
Type: Uganda, Bagshawe 669. Holotype: BM. Syn. of C. gomphophylla Baker; Basionym: *C. ugandensis* Rendle.
Celtis dysodoxylon **Thwaites**, Enum. Pl. Zeyl. 267 (1861).
Type: Sri Lanka, Thwaites c.p. 2563. PDA, BM, HAK, K, Isotype. Sri Lanka, India, Nepal, Bangladesh, Burma, Thailand, Indo-China and Malaysia.
Celtis edulis **Nakai**, Chosen Sanrin Kwaiho, No, 59. 23 (1930); Nakai, Fl. Sylvat. Koreana. 19: 70 (1932).
Type: Korea: Prokogen, Kanhoku. TH, TI. Prov. Kongen: Mt. Taikisan (S. Fukubara & K. Takaichi, Prov. Kanhoku: Meisen Jokomen.
Celtis ehrenbergiana **(Klotzsch) Liebm.**, Dansk. Vidensk. Selsk. Skrift. 5. 2. 339 (1851).
Type: Mexico: near Montezuma, Jan 1840, C. Ehrenberg 1114. Holotype: B. Basionym: *Momisia ehrenbergiana* Klotzsch. South America, Mexico, Haiti, Puerto Rico, southern USA.
Celtis elongata **Wall.**, Cat. N. 3692 (1831).
Type: Syn. of *Villebrunea integrifolia* Gaudich.
Celtis emuyaca **Metcalf**, Sunyatsenia 3, 112 (1936).
Celtis epiphylladena **Ortega**, Hort. Matr. 799 (1797); Nov. Pl. Descr. Dec. 79 (1789).
Type: Unknown (Berg & Dahlberg 2001). Not in MA. Syn. of *C. iguanaea* (Jacq.) Sarg.
Celtis eriantha **E.Mey. ex Planch.**, Ann. Sc. Nat. sér. 3. 5: 296 (1848).
Type: South Africa, Cape prov., near Graafreynet, 1000-1300 m, Burke in herb. Hook. OR DREGE. Syn. of *C. africana* Burm.f. South Africa.
Celtis eriocarpa **Decne**, Jacquem. Voy. Bot. 150 (1844).
Type: Between Nekki and Prountche. RAW, E. N.W.Himalaya.
Celtis espinosa **Larrañaga**, Publ. Inst. Hist. Geogr. Urug. 3: 42 (1924).
Nom. nud.
Celtis fengqingensis **Hu ex E.W.Ma**, Bull. Bot. Lab. North-East. Forest. Inst. 7: 122 (1980).
Celtis ferarum **Standl. & L.O.Williams**, Ceiba 1: 77 (1950).
Type: Nicaragua: Paul C. Standley no. 20384. ENAG, F, GH, US. Nicaragua, Loma entre matorrales, cerca de Condega. alt. 550 m.
Celtis ferruginea **(Wedd.) Miq.**, In Mart. Fl. Bras. 4, 1: 177 (1853).
Type: Brazil: Rio de Janeiro, Gaudichaud 1832, Casaretto 1846. Holotype: P-Photograph in MO,L, CL, D, BR, F, FI, G, MPU, PC, W. Syn. of *Momisia ferruginea* Wedd. Ann. Sci. Nat. Bot., sér. 3,18: 149.1852. Brasilia, Prope Rio de Janeiro, ibid. in monte Corcovado.
Celtis ferruginea **(Wedd.) Planch.**, in DC. Prodr. 17: 188 (1873).
Type: Brazil: Rio de Janeiro, Gaudichaud no 1832, Casaretto no 1846. Holotype: P.
Celtis ferruginea **Walp.**, Nov. Act. Nat. Cur. 19. Suppl. 1: 424 (1843).
Type: Syn. of *Ziziphus exserta* DC. in sylvulis ditionis Yungas reipublicae boliviensis. Bolivia.
Celtis flagellaris **Casar. ex Planch.**, in DC. Prodr. 17: 189 (1873).
Type: Syn. of *C. brasiliensis* (Gardner) Planch.
Celtis flexuosa **(Wedd.) Miq.**, in Mart. Fl. Bras. 4, 1: 181 (1853).
Type: Bolivia: La Paz: Prov. Yungas, Dec. 1846, Weddell 4421. Holotype: P; iso: P, PC, S. Syn. of *C. brasiliensis* (Gardner) Planch. Other syn.: *Momisia flexuosa* Wedd., Ann Sci. Nat. Bot., sér. 3, 18: 1951(852).

***Celtis flexuosa* Wedd. var. *glabrifolia* Griseb.**, Abh. Konigl. Ges. Wiss. Göttingen 24, 1: 85 (1879).
Type: Argentina: Salta: Oran, Oct 1873, Lorentz & Hieronymus 483. Holotype: GOET. Syn. of *C. ehrenbergiana* (Klotsch) Liebm.
***Celtis flexuosa* Planch.**, in DC. Prodr. 17: 192 (1873).
Type: Bolivia: La Paz, Prov. Yungas, Dec.1846, Weddell 4421.
***Celtis floridana* Rafin.**, New. Fl. Am. 3. 37 (1836-38).
***Celtis fluminensis* Carauta**, Atlas Soc. Biol. Rio de Janeiro 15, 1: 39 (1971).
Type: Brazil: Rio de Janeiro,1832 Gaudichaud 91. Holotype: P-Photograph in MO, L, CL, D, BR, F, FI, G, MPU, PC, W. Syn. of *C. brasiliensis* (Gardner) Other syn.: *Momisia ferruginea* Wedd., *C. ferruginea* (Wedd.) Miq.
***Celtis fragifera* A.Chev.**, Expl. Bot. Afr. Occ. Franc. 1. 588 (1917).
Type: Ivory Coast: Valley of the Moyen-Comoé river, between Tingouéla and Assikasso, Chevalier 22575. Holotype: P, iso: K. Nomen, syn. of *C. adolfi-friderici* Priemer ex Engl.
***Celtis franksiae* N.E.Br.**, in Dyer, Fl. Cap. 5, 2: 517 (1920).
Type: S.Africa, Natal, near Durban, Miss Franks in Herb.Wood 11725. Syn. of *C. mildbraedii*.
***Celtis fuscata* Rafin.**, New. Fl. Am. 3: 33 (1836-38).
***Celtis fuscata* Rojas**, Cat. Hist. Nat. corrient. 81 (1897).
***Celtis formosana* Hayata**, Journ. Coll. Sci. Univ. Tokyo 3 Art. 1, 272 (1911).
Type: Accepted. Taiwan.
***Celtis gardneri* Planch.**, Ann. Sc. Nat. sér. 3, 10 : 311 1848).
Type: Brazil: Alagoas, Rio Sao Francisco, Sao Pedro Island, Feb. 1838, Gardner 1406. Holotype: K, iso: P, S. Syn. of *C. iguanaea* (Jacq.) Sarg. Brazil.
***Celtis georgiana* Small**, Bull. Torrey Bot. Club 24: 439 (1897).
Type: America (north-central Georgia). Syn. of *Celtis tenuifolia* var. *georgiana* (Small) Fernald & B.G.Schub. and *Celtis pumila* var. *georgiana* Sarg. & *Celtis occidentalis* subsp. *georgiana* (Small) E. Murry. & *Celtis occidentalis* var. *georgiana* (Small) H. E. Ahles. Along or near streams, North-central Georgia.
***Celtis glabra* Noronha**, Verh. Batav. Gen. v. ed. 1 art. 4, 12 (1790).
Type: L. India: Kumaon.
***Celtis glabra* Planch.**, Ann. Sc. Nat. Bot. sér. 3, 10: 298 (1848).
Type: Upper India: Kumaon, Wallich 3695B. Holotype: LINN; iso: K.
***Celtis glabrata* Spreng.**, Syst. Veg. 5: 150 (1828).
Type: Mexico. Campeche: without locality, Apr., in herb. Humboldt s.n. Holotype: B; iso:UN. Syn. of *Mertensia laevigata* Kunth., *Momisia laevigata* (Kunth) F.Dietr., *Celtis aculeata* Sw. var. *laevigata* (Kunth) Planch.
***Celtis glabrata* Stev. ex Planch.**, Ann. Sc. Nat. sér. 3, 10: 285 (1848).
Type: Province Caucasus, Tauria, Stev. Dd. 1834, Besser, Georgia near Elisabethpol in herb. Hook. Syntypes: K. Accepted. Caucasus, Asia Minor.
***Celtis glomerata* Hochst.**, Flora 28. 87. (1845).
Type: South Africa. L, K, BR. Syn. of *Sponia guineensis* Hochst. Natal.
***Celtis glycycarpa* Mart. ex Miq.**, in Mart. Fl. Bras. 4, 1: 174, 1853.
Type: Brazil: Minas Gerais: Near Itambe' and Duas Pontes, Pohl s.n.; Minas Gerais: Praesidium S.Joan Baptistae, Martius s.n. Syntypes: M., photograph in MO and NY; U respectively. Syn. of *C. iguanaea* (Jacq.) Sarg.
***Celtis gomphophylla* Baker**, J. Linn. Soc. 12. 521 (1887).
Type: Madagascar, Baron 3697. Holotype: K; iso: BR, P. Accepted. Madagascar.
***Celtis gongshanensis* Xiang, W.Li & G.S.Fan**, Acta. Bot. Yunnanica 20, 2: 160 (1998).
Type: China South-Central, Collector: G. M.Feng 24523. PE. Holotype: KUN. Gongshan Xian, 2000 m.
***Celtis goudotii* Planch.**, Ann. Sc. Nat. Bot. sér. 3. 10, 312.1848.
Type: Colombia: Tolima: between Ibagu'e and Fusaguasuga, Goudot s.n. Holotype: K. Syn. of *C. iguanaea* (Jacq.) Sarg.
***Celtis grandidentata* Ten.**, Ind. Sem. Hort. Neap. 15 (1833).
Type: Syn. of *Celtis occidentalis* var. *grandidentata* Dippel.
***Celtis grewioides* Warb.**, Bot. Jahrb. Syst. 13. 287 (1891).
Type: Syn. of *Ziziphus angustifolia*. India, Burma,Thailand, Malaysia, Philippines, New Guinea.
***Celtis guineensis* Schum. & Thonn.**, Beskr. Guin. Pl. 160 (1827).
Type: Ghana. iso: C. Syn. of *Trema guineensis* (Schumach. & Thonn.) Ficalho. Tropical Africa, Madagascar, Arabia.
***Celtis hamata* Blume**, Mus. Bot. Lugd. Bot. 22: 72 (1856).
Type: Malaya. Syn. of *C. timorensis* Span. Malaya, India, Bangladesh.
***Celtis hamiltonii* Planch.**, Ann. Sc. Nat. Bot. sér. 3, 10: 301 (1848).
Type: India. Attran river, Hamilton s.n. Holotype: LINN.
***Celtis harperi* Horne ex Baker**, Bot. J. Linn. Soc. 20. 371 (1883).
Type: Fiji. GH, K, LE K. Mountain forests between Wai Wai and Lomaloma, Vanua Levu.

Celtis hashimotoi **Koidz.**, Acta Phytotax & Geobot. 1. 19 (1932).
Type: Japan: Hondo, C. Hashimoto. TH, TI. Syn. of *C. jessoensis* Koidz. Japonia, Honto, prov. Ohmi, Higashi-asaigun, Kusanomura, Kami-itanami, Yasakajinjia, Prov. Mimasaka, prov. Bittsiu, prov. Aki.

Celtis hasseltii **Planch.**, in DC. Prodr. 17: 185. (1873).
Type: Japan, Honto, Ohmi, Higashi, C. Hashimoto. K. Japan, Honto, prov. Ohmi, Higashi-asaigun, Kusanomura, Kami-itanami, Yasakajinjia, Prov. Mimasaka, prov. Bittsiu, prov. Aki.

Celtis helleri **Small**, Bull. Torrey Bot. Club 24: 439 (1897).
Type: Texas, near San Antonio, Collector: Mr. Heller, no 1587. Accepted. Syn.: *C. lindheimeri* Engelm. ex C.Koch.

Celtis henriquesii **Engl.**, Notizbl. Bot. Gart. Berlin 3. 22 (1900).
Type: Angola. Lectotypes: BM, K. Syn. of *C. africana* Burm.f. Africa: Benguella, in Jugo Chella alt. 800-1200m.

Celtis heterophyla **Rafin.**, New. Fl. Am. 3: 37 (1836-38).

Celtis hilariana **Planch.**, in DC. Prodr. 17: 189 (1873).
Type: Brazil. Minas Gerais: without locality, 1816-1821, Saint-Hilaire 1877. Holotype: P; iso: P. Syn. of *C. iguanaea* (Jacq.) Sarg.

Celtis hildebrandii **Soepadmo**, Fl. Males. Ser. 1, 8 (2): 63 (1977).
Type: Malesia, Molucas XXX(Buru, rare), New Guinea. BR, L, LAE, M, MAN. Malesia, Moluccas (Buru, rare), New Guinea, W & E parts, common, New Britain, in both primary and secondary forests at 0-1000 m.

Celtis holtzii **Engl.**, Engl. & Drude, Veg. der Erde 9: 12 (1915).
Type: Tanzania, Collector: holtz 1591. Holotype: B; photo in K. Syn. of *C. africana* Burm.f.

Celtis hottlei **Standl.**, Tropical Woods 20: 20 (1929).
Type: Honduras & British Honduras, Near Progreso, Dept. Yoro, April 4, 1929, W.D. Hottle 32. (Herb. Field Mus. 589282, Type: Yale 15610). Farm 43 near Progreso, April 2ed, 1929, Hottle 108 (Yale 15669)- British Honduras, Hillbank, July 1928, C. S. Brown xvii (Yale. A, F. Honduras, near Progreso, Hillbank.

Celtis hunanensis **Hand-Mazz.**, Anz. Akad. Wiss. Wien, Math.-Nat, 9: 53 (1922).
Type: China (Hunan).

Celtis hypoleuca **Planch.**, in DC. Prodr. 17: 183 (1873).
Type: In Nova Caledonia, Balansa n. 1665 and 1665 in Mus Paris. New Caledonia, Canala.

Celtis iguanaea (as iguaneus) **(Jacq.) Sarg.**, Silva North America 7: 64 (1895).
Type: Jamaica. Basionym: *Rhamnus iguanaeus* Jacq., Enum. syst. Pl. 16.1760. Other syn.: *Ziziphus iguanea* (Jacq.) Lam., Encycl. 3: 318 (1789) & *C. aculeata* Sw. America: Florida (USA) to Argentine.

Celtis ilicifolia **Engl.**, Pflanzenw. Ost-Afr. C. 160 (1895).
Type: Tsaydo River, Collector, Hildebr. No 2608. Holotype: B; iso: BO, BZF.

Celtis ingens **F.Muell.**, Fragm. Phyt. Australiae 4: 88 (1864).
Type: Australia, Hasting river, Richmond et Clarence River, at Edgecomb Bay, Sula, Sweer's Island. Holotype: MEL; iso: K, L. Syn. of *C. paniculata* (Endl.) Planch.

Celtis inglisii **Royle**, Illustr. Bot. Himal. 341 (1835/39).
Type: India, Kunaor, Royle s.n. Name, no description.

Celtis insularis **Rendle**, Journ. Bot. 3: 297 (1915).
Type: West tropical Africa, St. Thomas Island, Don, 35 Welwitsch, 6304, Qumtas 144, Princes Island, 1113. K. Syn. of *C. philippensis* Blanco. West Tropical Africa, St. Thomas Island, Princes Island.

Celtis integrifolia **Lam.**, Encyc. 4. 140 (1797).
Type: Senegal, Adanson 229 A. Holotype: P, photo in K. Syn. of *C. toka* (Forssk.) Hepper & J.R.I. Wood. Senegal to Uganda, Sudan, and Arabia.

Celtis ituriensis **De Wild.**, Rev. Zool. Afr. 9, Suppl. Bot. 4 (1921).
Type: Congo Republic, Bequaert 2153. Holotype: BR. Syn. of *C. adolfi-friderici* Engl. DR Congo (K).

Celtis jamaicensis **Planch.**, Ann. Sc. Nat. Bot. sér. 3. 290 (1848).
Type: Jamaica, Shakspeare s.n. in herb. Banks & MacFayden s.n. in herb. Hook. Syntypes: K.

Celtis japonica **Planch.**, in DC. Prodr. 17: 172 (1873).
Type: Japan, Small s.n., coll. Wright. Holotype: P. Basionym of *C. sinensis* var. *japonica* (Planch.) Nakai, Japan, China.

Celtis jessoensis **Koidz.**, Bot. Mag. Tokyo 27: 183 (1913).
Type: Japan, Ezo-enoki. A, TI. Accepted. Japan & Korea (in monte Hakuyozan prov. Zennan, silvis montium Chirisan prov. Zennan, in monte Keiryuzan prov. Chunan, in silvis Koryo prov. Keiki.

Celtis julianae **C.K.Schneid.** , in Sarg. Pl. Wils. 3: 265 (1916).
Type: China (Hupeh). A, B, K, NY, P, S. China (western Hupeh) Patung hsien, woodlands, alt. 900 -1100 m.

Celtis kajewskii **Merr. & Perry**, Journ. Arn. Arb. 32: 254 (1941).
Type: Bismark (New Britain), Solomon Islands, (East Australia), Guadalcanal, Berande, Kajewski 2445. January 1931. Holotype: A; iso: FU. Solomon Islands, Guadalcanal, Berande, in rain forest, New Britain (Keravat Experiment station, near Rabaul).

Celtis koidzumi **Nakai**, Bot. Mag. Tokyo 28: 265 (1914).
Type: Japan. Japan.

***Celtis koraiensis* Nakai**, Bot. Mag. Tokyo 23: 191 (1909).
Type: Korea, Sailhokumen prov., Kyongsan. A, TE. Accepted. Korea, N. China, Manchuria.
***Celtis kotschyana* Stev.**, Bull. Soc. Nat. Mosc. 30: 329 (1857).
***Celtis kraussiana* Bernh.**, Flora 28: 87 (1845).
Type: South Africa, Cape Province, Krauss. Holotype: K, in Hook herb.; iso: BM, G, K. Syn. of *C. africana* Burm.f. S. Africa: Tafelberg.
***Celtis kraussiana* Bernh. var. *stolzii*,** Feddes Repert. Beih. 40, 2: 64 (1932).
Type: Holotype: B; iso: BM, K.
***Celtis kunmingensis* Cheng & Hong**, Scientia Silvae 1: 12 (1967).
Type: China. China.
***Celtis labilis* C.K.Schneid.**, in Sarg. Pl. Wils. 3: 267 (1916).
Type: China, Western Hupeh: Changyang Hsien, A. Henry 3404. A, B, NY, P, S. Accepted. China: West Hupeh, Changyang Hsien, alt. 900 -1300 m.
***Celtis lactea* Sim**, Fl. Port. E. Afr. 97 (1909).
***Celtis laeta* Salisb.**, in DC. Prodr. 175. 1873.
***Celtis laevigata* (Kunth) Spreng.**, Syst. Veg.1: 932 (1824).
Type: Mexico: Campeche, no locality, Humboldt s.n. Holotype: B. Syn. of *C. iguanaea* (Jacq.) Sarg.
***Celtis laevigata* Willd.**, Enum. Hort. Berol. 67 (1814).
Type: Syn.: *C. mississipiensis*.
***Celtis laevigata* Willd.**, Berlinische Baumzucht, ed. 2: 81 (1811).
***Celtis laevigata* Willd. subsp. *reticulata* (Torr.) E.Murray**, Kalmia 13: 4 (1983).
Type: Basionym: *C. reticulata* Torr.
***Celtis laevigata* Willd. var. *anomala* Sarg.**, Bot. Gaz. 67: 225 (1919).
***Celtis laevigata* Willd. var. *appostita* Ashe**, Bull. Torrey Bot.Club 50: 361 (1923).
***Celtis laevigata* Willd. var. *brachphylla* Sarg.**, Bot. Gaz. 67: 225 (1919).
***Celtis laevigata* Willd. var. *brevipes* Sarg.**, Bot. Gaz. 67: 225 (1919).
***Celtis laevigata* Willd. var. *reticulata* (Torr.) L.D.Benson**, Amer. J. Bot. 30: 225. 1943.
Type: Syn. of *C. reticulata*.
***Celtis laevigata* Willd. var. *smallii* Sarg.**, Bot. Gaz. 67: 223 (1919).
Type: Basionym: *C. smallii* Beadle. Accepted. SE USA.
***Celtis laevigata* Willd. var. *texana* Sarg.**, Bot. Gaz. 67: 223 (1919).
Type: Basionym: *C. texana* Scheele. Accepted. SE USA.
***Celtis lamarckiana* Roem. & Schult.**, Systema veget. 6: 311 (1820).
Type: Martinique Martin (Pacific Ocean). BZF, J, E. Syn. of *Trema lamarckiana* (Roem. & Schult.) Blume.
***Celtis lanceolata* Parodi**, Ann. Soc. Cient. Argent. V. 5: 152 (1878).
Type: Paraguay: Caaguazú, 1863, Anon. s.n. Not traced (Berg & Dahlberg 2001). Possibly *Celtis brasiliensis*. Paraguay.
***Celtis lancifolia* (Wedd.) Miq.**, in Mart Fl. Bras. 4, 1: 175 (1853).
Type: Brazil: Rio Grand do Sul: without locality, 1833, Gaudichaud 1723. Holotype: P. Syn. of C. ehrenbergiana (Klotsch) Liebm. Basionym: *Momisia lancifolia* Wedd.
***Celtis lancifolia* Planch.**, in DC. Prodr. 17: 192 (1873).
Type: Brazil: Rio Grand do Sul: without locality, 1833, Gaudichaud 1723. Holotype: P. Basionym: *Momisia lancifolia* Wedd. Brazil: prov. Rio Grande.
***Celtis latifolia* Planch.**, in DC. Prodr. 17: 186 (1873).
Type: New Guinea. U, W. Aisuma Isl. near New Guinea, Malaysia, Philippines.
***Celtis laurifolia* Planch.**, in DC. Prodr. 17: 185 (1873).
Type: Java, Mt. Menara. FB. Syn. of *C. philippensis* Blanco. Indonesia: Java, Bantam.
***Celtis leveillei* Nakai**, Bot. Mag. Tokyo. 19: 266 (1914).
Type: Japan, China. TI, A. Accepted. Syn. *C. bungeana* var. *heterophylla* Lév., *C. sinensis* (non Pers.) Nakai pro parte. Japan, China, Korea.
***Celtis leveillei* Nakai var. *holophylla* Nakai**.
Type: Japan. Accepted. Japan.
***Celtis lima* Blanco**, Fl. Filip. ed. 1. 197 (1837).
Type: Syn. of *Trema blancoi* Blume.
***Celtis lima* Lam.**, Encycl. 4: 40 (1796).
Type: Syn. of *Trema lamarckiana*.
***Celtis lima* Sw.**, Prodr. Veg. Ind. occ. 53 (1788).
Type: Syn. of *Trema lima* Blume.
***Celtis lindheimeri* Engelm. ex C.Koch**, Dendro. 2, 1: 434 (1872).
Type: N. Mexico, Texas. Syn.: *C. helleri* Small.

***Celtis littoralis* Liebm.**, Vidensk Selsk. Skr. 5, 2: 337 (1851).
***Celtis liukiuensis* Nakai**, Bot. Mag. Tokyo. 27: 265 (1914).
Type: Japan. TAI. Syn. of C. *boninensis* Koidz. Japan.
***Celtis longifolia* Nutt**, N. Amer. Sylv. 1: 134 (1852).
Type: Syn. of *C. occidentalis* var. *integrifolia* Nutt.
***Celtis longifolia* Rafin.**, Atl. Journ. 177 (1833).
***Celtis loxensis* C.C.Berg**, Brittonia 53: 75 (2001).
Type: Ecuador. Loja: Rd. Catamayosan Pedro de la Bendita, track to hostería Bella Vista, km 3, secondary track to right, km 3.5, G.P.Lewis & C.C.Berg 3739. Holotype: LOJA, iso: AAU, MO, K, BG, AAU, QCA, QCNE. Accepted.
***Celtis lutea* Pers.**, Syn. Pl. 1: 292 (1805).
Type: Syn. of *C. australis* L.
***Celtis luzonica* Warb.**, Perkins, Frag. Fl. Philipp. 164 (1905).
Type: Philippines, Northen Luzon to Mindanao, Warburg 11912. US, PNH, B, E, HUG, BM, C, GH, L.
***Celtis macrophylla* Kunth**, Nov. Gen. et Sp. 2: 24 (1817).
Type: Syn. of *Trema macrophylla* (Kunth) Blume.
***Celtis madagascariensis* Boj.**, Hort. Maurit. 296 (1837).
Type: Nom. inval., nom nud. Syn. of *Trema orientalis* L.
***Celtis madagascariensis* Sattarian**, Blumea 50: 501 (2005).
Type: Madagascar: Toliara, Reserve d'Andohaleha, Phillipson 2938. Holotype: MO; iso: WAG. Madagascar. Nom. nov.: *Celtis malagasica* Sattarian.
***Celtis mairei* Lév.**, Feddes Repert. 13. 264 (1914).
Type: China: Yunnan, Tong-Tchouan. DAO, E. China: Yunnan near Long-Tan a Tong-Tchouan, 2500 m.
***Celtis malagasica* Sattarian**, This volume, nom nov. To replace *C. madagascariensis* Sattarian nom. inval.
Type: Madagascar: Toliara, Reserve d'Andohaleha, Phillipson 2938. Holotype: MO; iso: WAG.
***Celtis maritima* Rafin.**, Am. Monthy. Mag. 2. 44 (1817).
***Celtis mauritiana* Planch.**, Ann. Sc. Nat. sér. 3, 10: 307 (1848).
Type: Mauritius, Commerson. Holotype: K. Mauritius.
***Celtis membranacea* (Wedd.) Miq.**, Mart. Fl. Bras. 4, 1: 176 (1853).
Type: Brazil: Rio de Janeiro, 1831-1833, Gaudichaud 1081. Holotype: P; iso: P. Syn. of *C. iguanaea* (Jacq.) Sarg. Basionym *Momisia membranacea* Wedd. Brazil: prov. Goyaz.
***Celtis micrantha* (L.) Sw.**, Prodr. veg. Ind. Occ. 53 (1788).
Type: L. Basionym *Rhamnus micrantha* L. Syn. of *Trema micrantha*.
***Celtis microcarpa* Salzm. ex Planch.**, Ann. Sc. Nat. sér. 3. 10: 333 (1848).
Type: Syn. of *Trema micrantha* (L.) Blume.
***Celtis microphylla* Zipp. ex Blume**, Mus. Bot. Lugd. Bat. 2. 59 (1856).
Type: Syn. of *Trema timorensis* Blume.
***Celtis mildbraedii* Engl.**, Bot. Jahrb. Syst. 43. 309 (1909).
Type: Congo Republic, Mildbread 2897. Lectotype: B, BM, HBG, L, photo in K. Accepted. Tropical Africa from Ivory Coast to Tanzania and Angola.
***Celtis mindanaensis* Elmer**, Leaflets Philipp. Bot. 8. 2842 (1915).
Type: Mindanao: District of Davao, Mindanao, june, 1909, A.D.E. Elmer 10999. A, B, BM. Syn. of *C. philippensis Blanco*. Philippines, Mindanao.
***Celtis mississippiensis* Bosc.**, Lam. Encycl. Méth. Agr. 7. 577 (1821).
Type: Syn. of *C. laevigata* Willd.
***Celtis mollis* Humb. & Bonpl.**, Revisio Generum Plantarum 2: 634 (1891).
Type: Syn. of *Trema orientalis* var. *mollis* Kuntz.
***Celtis mollis* Humb. & Bonpl. ex Willd.**, Sp. Pl. ed. 4: 996 (1806).
Type: Syn. of *Trema micrantha* (L.) Blume.
***Celtis mollis* Wall.**, Wall. Cat. n. 7203 (1831).
***Celtis monoica* Hemsl.**, Biol Centr.-Am., Bot. 3. 139 (1883).
Type: Mexico.
***Celtis montana* Jungh. ex Planch.**, in DC. Prodr. 17: 193 (1873).
Material: Junghuhn s.n. BOG, L. Nomen nudum. Syn. of *Parasponia parviflora* Miq.
***Celtis morifolia* Planch.**, Ann. Sc. Nat. sér. 3. 10: 311 (1848).
Type: Brazil: Goia's: La Natividad, Dec 1839, Gardner 3426. Holotype: K; isotype (fragment): U. Syn. of *C. iguanaea* (Jacq.) Sarg.
***Celtis morifolia* Rafin.**, New Fl. Am. 3. 34 (1836-38).
Type:. Brazil: prov. Goyaz.
***Celtis mukii* Siebold & Zucc.**, Abh. Akad. Münch. 4. 3: 223 (1846).
Type: Japan.

***Celtis muku* Siebold**, Verh. Batav. Gen. 12. 28 (1830).
Type: Syn. of *Aphananthe aspera* Planch.
***Celtis multifolia* Elmer ex Merr.**, Enum. Philipp. Fl. Pl. 2. 32 (1923).
Type: Philippines: Northen Luzon to Mindanao and Palawan. US, PNH. Syn. of *C. philippensis* Blanco. Philippines: Northern Luzon to Mindanao and Palawan, Southeastern China and Taiwan to north eastern Australia.
***Celtis napalensis* Planch.**, Ann. Sc. Nat. sér. 3. 10: 298 (1848).
Type: Nepal. L. Syn. of *C. tetrandra* Roxb. Nepal.
***Celtis nervosa* Hemsl.**, Bot. J. Linn. Soc. 26: 450 (1894).
Type: Taiwan; Apes' Hill, Playfair 458. K, Li, Chen. Syn. of *C. tetrandra* Roxb. subsp. *sinensis* (Pers.). Taiwan.
***Celtis nymanii* K Schum.**, K. Schum & Lauterb. Nachtr. Fl. Deutsch. Südsee 240 (1905).
Type: Malaysia, Nyman 239. B. Syn. of *C. rigescens* (Miq.). New Guinea.
***Celtis obliqua* Moench**, Meth. 344 (1794).
Type: Syn. of *C. occidentalis* L.
***Celtis occidentalis* L.**, Sp. Pl. 1044 (1753).
Type: USA, Virginia. Accepted. N. America.
***Celtis occidentalis* L. subsp. *georgiana* (Small) E.Murray**, Kalmia 12. 19 (1982).
Basionym *C. georgiana* Small.
***Celtis occidentalis* L. subsp. *tenuifolia* (Nutt) E.Murray**, Kalmia 12. 19 (1982).
Basionym: *C. tenuifolia* Nutt.
***Celtis occidentalis* L. var. *aspera* Dippel**, Handb. Laubholzk 2: 44 (1892).
Basionym: *C. aspera* Dippel.
***Celtis occidentalis* L. var. *audibertiana* Dippel**, Handb. Laubholzk 2: 43 (1892).
Basionym: *C. audibertiana* Spach.
***Celtis occidentalis* L. var. *canina* Sarg.**, Bot. Gaz. 67: 217 (1919).
Basionym: *C. canina* Raf.
***Celtis occidentalis* L. var. *canina* (Pers.) Willd.**
***Celtis occidentalis* L. var. *crassifolia*n (Lam.) Dippel,** Handb. Laubholzk 2: 44 (1892).
Basionym: *C. crassifolia* Lam.
***Celtis occidentalis* L. var. *georgiana* (Small) H.E.Ahles**, J. Elisha Mitchell. Sci. Soc. 80: 172(1964).
Basionym: *C. georgiana* Small.
***Celtis occidentalis* L. var. *grandidentata* Dippel**, Handb. Laubholzk 2: 44 (1892).
Type: Basionym *C. grandidentata* Ten.
***Celtis occidentalis* L. var. *grandidentata* Spach**, Ann. Sci. Nat. Bot. Sér 2, 16: 40 (1841).
Type: Nom. superfl.
***Celtis occidentalis* L. var. *pumila* (Muhlenb.) Pursh,** Gray Manual ed. 2: 397 (1856).
Basionym: *C. pumila* Pursh. Accepted. N. America.
***Celtis occidentalis* L. var. *reticulata* (Torr.) Sarg.**, Cat. For. Trees 9: 126 (1884).
Basionym *C. reticulata* Torr.
***Celtis occidentalis* L. var. *serrulata* Spach**, Ann. Sci. Nat. (Paris) (sér 2) Bot. 16: 41 (1841).
***Celtis occidentalis* L. var. *submembranacea* Fernald**, Rhodora 37: 425. 1935.
Type: USA, Virginia, Knott's Island, Fernald & Long 3910. Holotype: GH. Accepted. USA, Virginia, N & S Carolina, Georgia.
***Celtis opaca* C.Moore ex Benth.**, Fl. Austral. 6. 157 (1873).
Type: Australia: N.S. Wales, N.Australia. Hasting, Clarence, and Richmond rivers, Beckler, C. Moore, London Exhibition 1862, n. 93. L, M. Syn. of *C. paniculata* (Endl.) Planch. Pacific Islands, Australia.
***Celtis opegrapha* Planch.**, Ann. Sc. Nat. sér. 3, 10: 294 (1848).
Type: South Africa, Cape Province. K, Isolecto. Syn. of *C. africana* Burm.f.
***Celtis orientalis* Hort. ex Steud.**, Nom. ed. 2. 1: 316 (1840).
Type: Syn. of *C. occidentalis* L.
***Celtis orientalis* Lam.**, Enc. 4: 138 (1796).
Type: Syn. of *Trema commersonii* Blume.
***Celtis orientalis* L.**, Sp. Pl. 1044 (1753).
Type: Syn. of *Trema orientalis*. Tropical Africa, Himalaya, India, Ceylon, Indo-China, W & S China, Australia, Polynesia.
***Celtis orientalis* Mill.**, Gard. Dict. ed. 8 (1768).
Type: Syn. of *C. australis* L.
***Celtis orientalis* Thunb.**, Fl. Jap. 114 (1784).
Type: Japan. Syn. of *C. sinensis*.
***Celtis orthocanthos* Planch.**, Ann. Sci. Nat. sér. 3, 10 : 309 (1848) & Miq. In Mart., Fl.bras. 4(1): 175.1853.
Type: Brazil: Bahia, without locality, Salzmann s.n. Holotype: K. Syn. of *C. aculeata*.

***Celtis pacifica* Planch.**, Ann. Sc. Nat. sér. 3. 10: 308 (1848).
Type: Pacific Ocean, Mathews no 95 in herb. Hook. K, BM. Syn. of *C. paniculata* (Endl.) Planch. Pacific ocean: Novaheoha.
***Celtis palauensis* Kanehira & Hatusima**, Bot. Mag. Tokyo. 53: 190 (1939).
Type: Japan. A, BO, FU. Syn. of *Trema integrifolia*. Japan.
***Celtis pallida* Torr.**, Rep. U.S. Mex. Bound. 2: 203.1859.
Type: USA, W Texas, Fort Duncan on Gulf of Mexico, Rio Grande, 1851-1852, Wright 1858. Lectotype: NY; iso: P. Syn. of C. ehrenbergiana (Klotsch) Liebm. Other syn.: *C. tala* var. *pallida* (Torr.) Planch. & *C. spinosa* var. *pallida* (Torr.) M.C. Johnst.
***Celtis pallida* Torr. subsp. *sericea* (Romanczuk) Romanczuk**, Darwiniana, 21, 2-4: 562 (1978).
Type: Argentina: Jujuy: Depto. San Pedro. San Lucas, 23 Jan 1976, Cabrera et al. 27532. Holotype: SI; iso: P. Syn. of C. chichape (Wedd.) Miq.
***Celtis pallida* Torr. subsp. *sericea* Romanczuk & M.A.Martinez**, Darwiniana, 21, 2-4: 562 (1978).
Type: Syn. of C. chichape (Wedd.) Miq.
***Celtis pallida* Torr. var. *discolor* Hunz. & Dottori**, Kurtziana, 9: 130 (1976).
Type: Argentina: Catamarca: Depto. Capayan, Sierra de Ambato,Quebrada de San Jeronimo, 5 km of Chumbicha, 19 Feb 1975, Hunziker et. al. 22774. Holotype: CORD. Syn. of *C. chichape* (Wedd.) Miq.
***Celtis pallida* (Endl.) Planch.**, Ann. Sc. Nat. Bot. sér. 3, 10: 305 (1848).
Type: Syn. of *Solenostigma paniculata* Endl. Norfolk Isl., Pacific Ocean.
***Celtis pallida* Planch.**, Ann. Sc. Nat. Bot. sér. 3. 10: 305 (1848).
Type: Australia, Pacific.
***Celtis paniculata* (Endl.) Planch.**, Ann. Sc. Nat. sér. 3, 10: 305 (1848).
Type: Australia, Pacific. K, BM. Accepted (J. Arn. Arbor. 67: 119 (1986). Australia, Malesia, New Guinea.
***Celtis parvifolia* A.Rich**, Fl. Cub. Fanerog. 2. 219.
Type: Cuba.
***Celtis parvifolia* Rafin.**, New. Fl. Am. 3. 36 (1836-38).
Type: Syn. of *C. occidentalis* L.
***Celtis patula* Rafin.**, New Fl. Am. 3. 37 (1836-38).
Type: Syn. of *C. reticulata*.
***Celtis pavonii* Planch.**, Ann. Sc. Nat. sér. 3. 10: 313 (1848).
Type: Peru, without locality, Ruiz & Pavon s.n. Holotype: K, in herb. Hook, specim. Ex herb. Lambert en Museo Berolinensi sub *C. biflorae*, iso: G, photograph in MO, =same type collection as for *M. dichotoma* Klotzsch. Syn. of *C. iguanaea* (Jacq.) Sarg. Peru.
***Celtis petenensis* Lundell**, Bull. Torr. Bot. Cl. 69: 386. 1942.
Type: Guatemala, C.Llundell 4306 Type in University of Michigan Herbarium. Holotype: MICH; iso: A, BM, C, F, GH, K, LCU. Guatemala: Peten: Lake Yaxha, on ruins of Topoxte.
***Celtis philippensis* Blanco**, Fl. Filip.ed. 1: 197 (1837), ed. 2: 139 (1845), ed. 3: 249 (1877).
Type: Philippines: Malaitmo. US, PNH, WAG. Syn.: *C. philippinensis* Benth., *C. strychnoides* Planch. Indian Ocean, Burma, S.E. China, Hong Kong, Taiwan, Indo-China, Thailand, Malesia, Solomon Isls.
***Celtis philippensis* Blanco var. *wightii* (Planch.) Soepadmo**, Fl. Males. Ser. 1, 8 (2): 62 (1977).
Basionym: *C. wightii*. Relegated to the synonymy of *C. wightii* Planch.
***Celtis philippinensis* Hayata,** Hayata Enum. Pl. Formos. 369 (1906), (non Blanco).
Specimen examined by Hayata: Taiwan, Kelung and Pachina, Makino s.n. anno 1896 (TAI). Taiwan. Syn. of *C. philippensis* Blanco
***Celtis planchoniana* K.I.Christensen**, Fl. Hellenica 1: 54 (1997).
Type: Ukraine: Crimea. Lectotype: H, B, BR. Syn. of *C. glabra* Stev. ex Planchon, *C. tourneforti* Lam var. *glabrata* Boiss. S. Jugoslavia and Bulgaria, NE Greece, Turkey, Syria, N. Iraq and Iran.
***Celtis platycaulis* Greenm.**, Proc. Amer. Acad. Arts 39: 78 (1903).
Type: Mexico: Morelos, near Yantepec, 5 Jul. 1901, Pringle 8535. Holotype: GH.; iso: G, GOET, M, NY, P, US. Syn. of *C. iguanaea* (Jacq.) Sarg. Other syn.: *Momisia platycadis* (Greenm.) Rose & Standl.
***Celtis politoria* Wall.**, Wall.Cat. n. 3693 (1831).
Type: Nepal & Kumaon,Thompson 838. RAW, syntype. Syn. of *Trema politoria*. India: Himalaya, S.W. China: Yunnan.
***Celtis polycarpa* Lév.**, Feddes Repert. 11: 296 (1912).
Type: China: Kweichau, Cavalerie no 3790. Holotype: P; iso: A, G, K.
***Celtis polyclada* Peter**, Feddes Repert. Beih. 11. 2. Anhang. 1 (1932).
Type:.
***Celtis prantlii* Priemer ex Engl.**, Nobtizbl. Bot. Gart. Berlin 3: 23 (1900).
Type: W. Africa. K. Accepted. West Africa.

Celtis prantlii **Priemer ex Engl. f.** ***parvifolia*** **Hauman**, Bull. Jard. Bot État 16: 411 (1942).
Type: DR Congo: Bokoboli, Claessens 612; between Amadia and Poko, Lebrun 3074; La Kulu, Vandenbranden 668; Luja, s.l., s.n. Syntypes: BR. Syn. of *C. prantlii* Priemer ex Engl. DR Congo.
Celtis prantlii **Rendle**, Fl. Trop. Afr., ed. Prain, 6, 2: 8 (1916).
Type: Annobon Isl. Syn. of *C. rendleana* G. Taylor.
Celtis procera **Salisb.**, Prodr. 175 (1796).
Type: Syn. of *C. occidentalis* L.
Celtis pruniputaminea **E.W.Ma**, Bull. Bot. Lab. North.-East Forest Inst. 1980, 7: 123 (1980).
Type: China: Kweichau. P, A, G.
Celtis pubescens **(Kunth) Spreng.**, Syst. Veg. 1: 931 (1824).
Type: Ecuador: Guatas, Guayaquil, Feb 1802, Humboldt s.n. Holotype: B, Photograph in NY; so: P. Syn. of *C. iguanaea* (Jacq.) Sarg.; Other syn.: *Mertensia pubescens* Kunth, Nov. Gen. Sp.2: 26 (folio)(1817); Schult., Syst.Veg. 6: 312.1820; *Momisia pubescens* (Kunth) Spreng., Nachtr. Vollst. Lex. Gaertn. Bot. 5: 123 (1819).
Celtis pubescens **Kunth**, Nov. Gen. et Sp. 2: 32 (1817).
Celtis pubescens **S.Y.Wang & C.L.Chang**, J. Henan Agric. Coll. 1980, 2: 7 (1980) & Fl. Henan 1: 268 (1981).
Type: China. China: Southeast (Henan).
Celtis pubescens **(Kunth) Planch var.** ***chichape*** **(Wedd.) Baehni**, Candollea 7: 201 (1937).
Type: Bolivia: Santa Cruz: Santa Cruz de la Sierra (Prov.Cordillera), Nov -Dec 1845, Weddell 3610. Holotype: P, photograph in MO; iso: MPU, P. Syn. of *Momisia chichape* Wedd, Ann. Sci. Nat.Bot.,sér. 3,18: 193.1852.
Celtis pumila **Pursh**, Fl. Amer. Sept. 1: 200 (1814).
Type: America: Maryland and Virginia. Basionym of *C. occidentalis* var. *pumila* (Pursh) A.Gray & C. *occidentalis* var. *pumila* Dippel & *C. mississippiensis* var. *pumila* Mack & Bush in Mack.
Celtis pumila **Pursh var.** ***deamii*** **Sarg.**, Bot. Gaz. 67: 228. (1919).
Celtis pumila **Pursh var.** ***georgiana*** **Sarg.**, Bot. Gaz. 67: 227. (1919).
Type: Syn. of C. georgiana Small.
Celtis punctata **(Urb. & Ekman) Urb. & Ekman**, Arkiv. Bot. 22A, 8: 14 (1929).
Type: Haiti, Montagnes du Trou d'Eau, near Glore, 22 July 1924, Ekman H.1041. Holotype: B, iso: S. Syn. of *C. ehrenbergiana* (Klotsch) Liebm. Basionym: *Sarcomphalus punctatus* Urb. & Ekman.
Celtis rendleana **G.Taylor**, Exell, Cat. Vasc. Pl. S. Tome 302 (1944).
Type: Angola: Welwitsch 6302. Holotype: BM, iso: K. Syn. *of C. prantlii* Priemer ex Engl.
Celtis reticulata **Boorsma**, Bull. Dep. Agric. Ind. Neerl. 7: 32 (1907), Sphalm.
Type: GH, NY. Syn. of *C. laevigata* subsp. *reticulata* (Torr.) E. Murray.
Celtis reticulata **Hook. f. & Thomson ex Planch.**, in DC. Prodr. 17: 209 (1873).
Type: Syn. of *Gironniera reticulata*. N. America.
Celtis reticulata **Torr.**, Ann. Lyceum. Nat. Hist. New York 2: 247 (1828).
Type: N. America, N. Mexico. Accepted. Basionym of *C. occidentalis* var. *reticulata* (Torr.) L.D.Benson & *C. occidentalis* subsp. *reticulata* (Torr) E.Murray, other syn.:*C. reticulata* var. *vestita* Sargent.
Celtis reticulata **Torr. var.** ***vestita*** **Sarg.**, Bot. Gaz. 67: 221 (1919).
Type: America. Syn.*: C. reticulata* Torr.
Celtis reticulosa **Miq.**, in Pl. Jungh. 69 (1851).
Type: Syn. of *C. cinnamomea*, *C. timorensis* Span.
Celtis rhamnifolia **Presl**, Bot. Bemerk. 37 (1845).
Type: South Africa without locality, Zeyher no. 314. Syn. of *C. africana* Burm.f.
Celtis rhamnoides **DC. ex Planch.**, in DC. Prodr. 17: 189 (1873).
Type: Syn. of *C. brasiliensis*.
Celtis rhamnoides **Willd.**, Sp. Pl. ed. 4: 998 (1806).
Type: Sp. Pl. 4: 998 (1806) C. Commelin, Horti Med. Amstel.ed.3 t. 73 (1724). Syn. of C. iguanaea (Jacq.) Sarg.
Celtis rigescens **Planch.**, in DC. Prodr. 17: 182 (1873).
Type: Sumatra. NY, U, US, W. Syn. of *C. sumatrana* Planch. Sumatra, Prov. Palembang.
Celtis rigida **Blume**, Bijdr. 486 (1824).
Type: Syn. of *Trema rigida Blume*.
Celtis rigida **D.Parodi**, An. Soc. Ci. Argent. 5: 153 (1878).
Type: Paraguay: Central, Asunción, Anon. s.n. Not traced (Berg & Dahlberg 2001). Possibly not *Celtis*. Paraguay.
Celtis riparia **Kunth**, Nov. Gen. et Sp. 2: 28 (1817).
Type: B, K. Syn. of *Trema riparia* Kunth.
Celtis riparia **Liebm.**, Vidensk. Selsk. 5. 2. 337 (1851).
Type: Syn. of *C. caudata*.
Celtis rockii **Rehder**, Journ. Arn. Arb. 12: 199 (1933).
Type: China: Yunnan, region of Tungshana. Ti, A. China. Yunnan: region of Tungshan drainage basin, east of Likiang.

***Celtis rostrata* Zipp. ex Span.**, Linnaea 15: 343 (1841).
Type: Syn. of *Sponia rostrata*.
***Celtis roxburghii* J.O.Voigt**, Hort. Suburb. Calcutt. 294 (1845).
Type: East India. A, BM, BR, CAL, E, G. Syn. of *C. trinervia* Koord.
***Celtis roxburghii* DC. ex Planch.**, Ann. Sc. Nat, sér. 3, 10 : 302 (1848).
Type: Syn. of *C. tetrandra*.
***Celtis rubrovenia* Elmer**, Leaflets Philipp. Bot. 2. 464 (1908).
Type: Philippines: Luzon, Vidal 1330, Loher 5037, Elmer 6040, 8775, Vanoverbergh 2578. A, B, DS, Accepted. E. Philippines (Luzon), Malesia, New Guinea.
***Celtis rufescens* Banks ex Planch.**, Ann. Sc. Nat, sér. 3, 10 : 334 (1848).
Type: Jamaica, Hartweg no. 1559. BM, NY. Syn. of *Trema micrantha* (L.) Blume. Jamaica.
***Celtis rugosa* A.Chev.**, Expl. Bot. Afr. Occ. Franc. 1. 589 (1920).
Type: Ivory Coast: Bouroukrou, railroad km 92, 20 Dec. 1906 - 20 Jan. 1907, Chevalier 16130 & Anoumaba forest, railroad km 140, 12-20 Nov. 1909, Chevalier B. 22393. Syntypes: P. Syn. of *C. zenkeri* Engl. Guinea, Ivory Coast.
***Celtis rugosa* Rydb.**, Bull. Torrey Bot. Club 39: 304 (1912).
Type: Syn.: *C. rugulosa* Rydberg. USA, Colorado.
***Celtis rugosa* Willd.**, Sp. Pl. ed. 4. 996 (1806).
Type: Syn. of *Trema rugosa*.
***Celtis rugulosa* Rydb.**, Fl. Rocky Mts. 207 (1917).
Type: A, AS, MT, NEB, NY. Syn. of *C. rugosa*.
***Celtis salicifolia* Rafin.**, New Fl. Am. 3: 34 (1836-38).
Type: Syn. of *C. mississippiensis*.
***Celtis salomonensis* Rech.**, Denkschr. Akad. Wiss. Wien. 1913, 84: 532 (1914).
***Celtis salvatiana* C.K.Schneid.** , in Sarg. Pl. Wils. 3: 283 (1916).
Type: China: Yunnan. TI. China.
***Celtis scabra* Casar. ex Planch.**, in DC. Prodr. 17: 204. (1873).
Type: Syn. of *Trema carinata* Blume.
***Celtis scabra* Hort. ex Dippel**, Handb. Laubholzk. 2. 44 (1822).
Type: Syn. of *C. occidentalis* L.
***Celtis schiedeana* Schlecht**, Linnaea 7: 140 (1832).
Type: Nom. nud. Syn. of *Trema micrantha* (L.) Blume.
***Celtis schippii* Standl.**, Field Mus. Nat. Hist. Botanical ser. 12: 409 (1936).
Type: British Honduras, Temash River, in primary forest, March 25, 1935, W.A.Schipp 1322. A, B, BM, BKL. Syn. of *Sparrea schippii* (Standl.) Hunz. & Dottori (Ulmaceae). Honduras.
***Celtis scotellioides* A.Chev.**, Expl. Bot. Afr. Occ. Franc. 1. 590 (1920), nomen.
Type: Ivory Coast: Haute-Sassandra, between Droupleu and Zoanlé, 5 May 1909, Chevalier 21459. Holotype: P; iso: K. Syn. of *C. prantlii* Priemer ex Engl.
***Celtis sellowiana* Miq.**, in Mart. Fl. Bras. 4, 1: 179 (1853).
Type: Brazil: In Brasiliae australiore, Sellow s.n. Holotype: U: iso: P, US. Syn. of C. ehrenbergiana (Klotsch) Liebm. Other syn.: *C. tala* var. *selloviana* (Miq.) Kuntze. Brazil, Rio Grande.
***Celtis sellowiana* Miq. f. *praecox* Lorentz**, Not published.
Type: Argentina: near Córdoba, Estancia Germanica, Jun.-Dec. 1874, Lorentz 133. GOET, MPU, P. Syn. of *C. ehrenbergiana* (Klotsch) Liebm.
***Celtis sericea* M.C.Romanczuk**, Hickenia 1, 2: 8 (1976).
Type: Argentina: Jujuy: depto. San Pedro, San Lucas, 23 jan 1976, Cabrera et al. 27532. Holotype: SI; iso: P. Syn. of *C. chichape* (Wedd.) Miq. Other syn.: *C. pallida* subsp. *sericea* (Romanczuk) Romanczuk.
***Celtis serotina* Planch.**, Ann. Sc. Nat. Bot. sér. 3, 10: 301 (1848).
Type: India, Nilgiri Mts, Gardner in herb. Hook. Holotype: K, W. Syn. of *C. tetrandra*. India, Burma, Indo-China, Malaysia.
***Celtis serrata* Hort. ex Dippel**, Handb. Laubholzk. 2: 43 (1822).
Type: Syn. of *C. australis* L.
***Celtis serrata* Hort. ex Ettingsh.**, Blatt-Skel. Dikot. 26. t. 3, fig 14 (1861).
***Celtis shortii* Planch.**, Ann. Sc. Nat, sér. 3, 10: 292 (1848).
Type: North America, Short, in herb. Hook. Holotype: K. DWC, GH, L, MO, W.
***Celtis similis* Merr. & Perry**, Journ. Arn. Arb. 22. 253. (1941).
Type: New. Guinea: Balim River, Brass & Versteegh no 11168. A, AMES, B, BM, BR, F, GH. New Guinea.
***Celtis sinensis* Pers.**, Syn. Pl. 1: 286 (1805).
Type: China. KAO, KW, L, LU. Accepted. China, Korea, Japan, Taiwan.
***Celtis sinensis* Pers. var. *japonica* (Planch.) Nakai**.
Type: Basionym: *C. japonica* Planch. Japan, Korea, China. Accepted by some authors.

Celtis sinensis **Planch.**, Ann. Sc. Nat. sér. 3, 10: 286 (1848).
Type: China. China.
Celtis sinensis **Willd.**, Enum. Hort. Berol. Suppl. 67 (1814).
Type: Japan. Japan.
Celtis smallii **Beadle**, Small, Fl. S. E. U. 365 (1903).
Type: USA: Tennessee to Georgia and Alabama. U. Basionym of *C. lavigata* var. *smallii* Sarg. USA: North Carolina and Tennessee to Georgia and Alabama.
Celtis solenostigma **Unwin**, West African Forests & Forestry 246 (1920).
Type: Nigeria. W, S, K, N. Abeokuta, Ibadan, Benin, Owerri, Ogoja provinces of Nigeria in the mixed deciduous forest zone.
Celtis soyauxii **Engl.**, Notizbl. Bot. Gart. 3: 23 (1900).
Type: Congo Republic: Soyaux 202 (Lectotype: B; iso: K) & Angola, Cuanza Norte, Welwitsch 6285 (Paratype: BM, COI, E, COI, K. Syn. of *C. zenkeri*. Loango: Tschintschocho, Bergwald Nuzala. Angola.
Celtis spinosa **Ruiz ex Miq.**, in Mart. Fl. Bras. 4, 1: 182 (1853).
Type: Brazil, no locality, Sellow s.n. Holotype: B. Syn. of *C. iguanaea* (Jacq.) Sarg.
Celtis spinosa **Ruiz ex Miq. var. *pallida* (Torr) M.C.Johnst.**, Southw. Naturalist 2(4): 172 (1957).
Basionym: *C. pallida* Torr. Type: USA Texas: Rio Grande, 1851-1852, Wright 1858. Lectotype [M.C.Johnston]. Syn. *of C. ehrenbergiana* (Klotsch) Liebm.
Celtis spinosa **Ruiz ex Miq. var. *weddeliana* (Planch.) Baehni**, Candollea 7: 204 (1936).
Type: Argentina: Corrientes: without locality, Feb. 1832, Bonpland 1211. P. Syn. of *C. ehrenbergiana* (Klotsch) Liebm. Other syn.: *C. tala* var. *weddeliana* Planch.
Celtis spinosa **Spreng.**, Syst. Veg. 1: 932 (1824.).
Type: Brazil. Without locality, Sellow s.n. Holotype: B. Brazil.
Celtis spinosa **Ruix & Pav.**, see Planch., in DC., Prodr. 17: 187 (1873).
Type: Syn. of *C. iguanaea* (Jacq.) Sarg.
Celtis spinosissima **(Wedd.) Miq.**, in Mart. Fl. Bras. 4, 1: 176 (1853).
Type: Brazil: Rio de Janeiro, Aug. 1828, Gay s.n. Holotype: P, photograph MO. Syn. of *C. iguanaea* (Jacq.) Sarg. Prov. Rio de Janeiro, Augusto.
Celtis strychnoides **Planch.**, Ann. Sc. Nat. sér. 3, 10: 306 (1848).
Type: Australia. DNH, TEX, TPV. Syn. of *C. philippensis* Blanco.
Celtis stuhlmanni **Engl.**, Notizbl. Bot. Gart. 3: 23 (1900).
Type: Tanganyika: Uluguru Mts., Stuhlmann 8703. Lectotype: B, isolecto: K. Syn. of *C. zenkeri* Engl.
Celtis subdentata **E.Mey. ex Planch.**, Ann. Sc. Nat. Bot. sér. 3, 10: 341 (1848).
Type: South Africa: distr. Somerset, Mt. Enon 1000-2000 ft. Holotype: P; iso: K. Syn. of *Chaetachme aristata* Planch.
Celtis sumatrana **(Miq.) Planch.**, in DC. Prodr. 17: 181 (1873).
Type: North Sumatra, prov. Angkol, forest, Junghuhn s.n. Basionym: *Solenostigma sumatranum* Miq. Holotype: U. Indonesia, Sumatra.
Celtis swartzii **Planch.**, Ann. Sc. Nat. Bot. sér. 3, 10: 304 (1948).
Type: Jamaica, Swartz . NY, K. Jamaica.
Celtis taiyuanensis **E.W.Ma**, Bull. Bot. Lab. North-East. Inst. 1980, 7: 124 (1980).
Type: China. A, GH, US, DS. China.
Celtis taiwanna **Hayata**, Journ. Coll. Sci. Univ. Tokyo 3 Art. 1: 272 (1911).
Type: Japan, Koshun: Naibun, Collector: G. Nakahara, Feb. 1907, Shizangan, Kelung, et Pikaku, T. Makino, 1896. TI, MAK. Syn.: *Celtis philippinensis* Hayata. Hayata, Enum. Pl. Formos. p. 369, (non Blanco). Koshun: Naibun, Shizangan.
Celtis tala **Gill. ex Planch.**, Ann. Sc. Nat. sér. 3, 10: 310 (1848).
Type: Argentina, prov. of San Luis, Gillies s.n. Lectotype: K. Syn. of *C. ehrenbergiana* (Klotsch) Liebm.
Celtis tala **Gill. ex Planch. var. *tala* Gill. ex Planch.**, Ann. Sc. Nat. sér. 3, 10: 310 (1848).
Type: Bolivia: Tariya, near Palo, Mar. 1910, Herzog 1805a; Tariya, Río Pilcomayo, Nov. 1910, Herzog 1096; Tariya, between Ipaguassú and Fontín d'Orbigny, Nov. 1910, Herzog 1071. Syntypes: G?, G & S, Z resp. Syn. of *C. chichape* (Wedd.) Miq.
Celtis tala **Gill. ex Planch. var. *tala* Gill. ex Planch. f. obtusata Chodat & Hassl.**, Bull. Herb. Boiss. sér. 2, 3: 348 (1903).
Type: Paraguay: near Concepción, Sept. 1901-1902, Hassler 7295. Holotype: G; iso: MPU, NY, P. Syn. of *C. ehrenbergiana* (Klotsch) Liebm.
Celtis tala **Gill. ex Planch. var. *chichape* (Wedd.) Planch.**, in DC. Prodr. 17: 191 (1873).
Type: Bolivia: Santa Cruz: Santa Cruz de la Sierra (Prov.Cordillera), Nov -Dec 1845, Weddell 3610. Holotype: P, photograph in MO; iso: MPU, P. Syn. of *C. chichape* (Wedd.) Miq.

Celtis tala **Gill. ex Planch. var.** ***chichape*** **(Wedd.) Planch. f. subpilosa Kuntze**, Rev. Gen. Pl. 3, 3: 294 (1898).
Type: Argentina: Santiago del Estero, Pinto, Oct. 1892, Kuntze s.n. Holotype: NY; iso: NY. Syn. of *C. ehrenbergiana* (Klotsch) Liebm.
Celtis tala **Gill. ex Planch. var.** ***chichape*** **(Wedd.) Planch. f.** ***subtomentosa*** **Kuntze**, Rev. Gen. Pl. 3, 3: 294 (1898).
Type: Argentina: Salta, Orán, Oct. 1873, Lorentz & Hieronymus 3. Holotype: NY; iso: GOET, S. Syn. of *C. ehrenbergiana* (Klotsch) Liebm.
Celtis tala **Gill. ex Planch. var.** ***gillesiana*** **Planch.**, (typical variety), in DC. Prodr. 17: 191 (1873).
Type: Argentina, prov. of San Luiz, Gillies s.n., Montevideo and Buenos Aires, Capt. King s.n., Hort. Algeriensis as Celtis du Paraguay, herb. Durand. Syntypes: K, K and P respectively. Lectotype: K. Syn. of *C. ehrenbergiana* (Klotsch) Liebm.
Celtis tala **Gill. ex Planch. var.** ***gaudichaudiana*** **Planch.**, in DC. Prodr. 17: 191 (1873).
Type: Brazil: Rio Grande do Sul, no locality, 1833, Gaudichaud 1732. Holotype: P. Syn. of *C. ehrenbergiana* (Klotsch) Liebm.
Celtis tala **Gill. ex Planch. var.** ***pallida*** **(Torr.) Planch.**, in DC. Prodr. 17: 191 (1873).
Type: USA, W. Texas, Fort Duncan on Gulf of Mexico, Wright 1858 & Port Lavaca, Trecul 1148. Syntypes: P. Syn. of C. *ehrenbergiana* (Klotsch) Liebm. Basionym: *C. pallida* Torr.
Celtis tala **Gill. ex Planch. var.** ***selloviana*** **(Miq.) Kuntze**, Revis. Gen Pl. 3. Pt. 2: 294 (1898) as *sellowiana*.
Basionym: *C. selloviana* Miq.
Celtis tala **Gill. ex Planch. var.** ***weddelliana*** **Planch.**, in DC. Prodr. 17: 191 (1873).
Type: Argentina.Corrientes: without locality, Feb 1832, Bonpland 1211. Lectotype: P. Syn. of *C. ehrenbergiana* (Klotsch) Liebm. Other syn.: *C. spinosa* var. *weddelliana* (Planch.) Baehni.
Celtis tenuifolia **Nutt.**, Gen. N. Amer. Pl. 1: 202 (1818).
Type: N.America. Syn. of *C. occidentalis* subsp. tenuifolia (Nutt) E.Murray, *C. georgiana* Small, *C. occidentalis* L. var. *georgiana* (Small) Ahles; *C. pumila* Pursh var. *georgiana* (Small) Sargent; *C. tenuifolia* var. *georgiana* (Small) Fernald & B.G. Schubert. N. America.
Celtis tenuifolia **Rafin.**, New. Fl. Am. 3. 36 (1836-38).
Type: Syn. of *C. occidentalis* L.
Celtis tenuifolia **Rafin. var.** ***tenuifolia*** **Nutt.**, Gen. N. Amer. Pl. 1: 202 (1818).
Celtis tenuifolia **Rafin. var.** ***georgiana*** **(Small) Fernald & B.G.Schub.**, Rhodora 50: 16 (1948).
Type: USA: Georgia. Basionym: *C. georgiana* Small.
Celtis tenuifolia **Rafin. var.** ***soperi*** **B. Boivin**, Naturaliste Canad. 94: 622 (1967).
Type: Canada: Ontario, Burcher, Soper 2200. Holotype: BOA.
Celtis tessmannii **Rendle**, Journ. Bot. 53: 297 (1915).
Type: Equatorial Guinea: inland, Mabungo 450, m, Tessmann B25 (B). Near Celtis zenkeri. W, B. Accepted. West Africa, Eq. Guinea, Gabon.
Celtis tetrandra **Roxb. f.** ***pendula*** **Y.Q.Zhu**, Bull. Bot. Res. North -East. Forest. Univ. 20: 7 (2000).
Type: China (Shandong). North-Central China.
Celtis tetrandra **Wall.**, Wall. Cat. n. 3695 F (1831).
Type: Holotype: K-Wall. Syn. of *Villebrunea integrifolia*.
Celtis tetrandra **Roxb.**, Hort. Beng. 21 (1814); Fl. Ind. 2, 2: 63 (1832).
Type: Nepal, Hamilton n. 1802. K. Himalaya (Kumaon to Bhutan), Khasia, Deccan and Malaysia, China.
Celtis tetrandra **Roxb. subsp.** ***sinensis*** **(Pers.)Y.C.Tang**, Acta Phytotax. Sin. 17, 1: 51 (1979).
Type: Berlandierii. Syn. of *C. nervosa* Hemsl. Basionym: *C. sinensis* Pers.
Celtis texana **Scheele**, Linnaea 22: 146 (1849).
Type: America, Lindheimer. BM, A, ARIZ, B, C, CAL, L. Syn. of *C. laevigata* var. *texana* (Scheele) Sarg. USA: Texas.
Celtis tikalana **Lundell**, Wrightia 2: 50 (1960).
Type: Guatemala, C.L. Lundell no 16083. A, BM, C, F, LCU, MO, NY. Guatemala.
Celtis timorensis **Span.**, Linnaea 15: 343 (1841).
Type: Timor. Holotype: L; isotype: K. Indonesia: Timor Mts.
Celtis toka **(Forssk.) Hepper & J.R.I.Wood**, Kew Bull. 38: 86 (1983).
Type: Senegal. Holotype: P-JU, G, PJU, P-LA. Accepted. Basionym: *Ficus toka* Forssk. Somalia, Senegal, Chad, Cameroon, Central African Republic, Sudan, Ethiopia, Uganda, Yemen.
Celtis tomentosa **Roxb.**, Hort. Beng. 86 (1814); Fl. Ind. 2, 2: 66 (1832).
Type: Syn. of *Trema amboinensis* Willd.
Celtis tournefortii **Lam.**, Encycl. méth. 4: 138 (1797).
Type: Turkey. L, K. Syn. of *C. australis* L. Balkan, Anatolia, N Iraq, W Iran, accepted by some authors.
Celtis trichocarpa **Cheng & E.W.Ma**, Bull. Bot. Lab. North-East. Forest. Inst. 1980 (7): 121 (1980) as "*tirchocarpa*".
Type: China. China.

Celtis triflora **(Klotzsch) Ruiz ex Miq.**, in Mart. Fl. Bras. 4, 1: 181 (1853).
Type: Peru. Pasco: Pozuzo, Ruiz & Pavón s.n. Holotype: B, photograph in MO; iso: P. Basionym: *Momisia triflora* Ruiz ex Klotzsch, Linnaea 20: 537 (1847). Syn. of *C. tala*
Celtis trinervia **Koord.**, Exkursionsfl. Java 2: 76 (1912).
Type: Syn. of *C. roxburghii* J.O. Voigt & *Bosea trinervia* Roxb. (Amaranthaceae). Indonesia, Malaysia, Himalaya, Andamans, Sri Lanka, Australia.
Celtis trinervia **Lam.**, Encycl. Méth. Bot. 4: 140 (1797).
Type: Guatemala, Santo Domingo. Accepted. Syn. of *Sponia trinervia* (Lam.) Decne, *C. swartzii* Planch. Southern Mexico, Guatemala, Sto Domingo.
Celtis tupalangi **Vassilcz.**, Not. Syst. Herb. Inst. Bot. Acad. Sci. URSS 18: 13 (1957).
Celtis ugandensis **Rendle**, Journ. Bot. 64: 341 (1906).
Type: Uganda: Entebbe, Bagshawe 669. Holotype: BM. Syn. of *C. gomphophylla* Baker. Uganda.
Celtis urticifolia **Rafin.**, New Fl. Am. 3: 32 (1836-38).
Type: Syn. of *C. occidentalis* L.
Celtis usambarensis **Engl.**, Bot. Jahrb. Syst. 63: 309 (1909).
Type: Tanganyika, E. Usambara, on Bomole about 1000 m Zimmermann in Herb. Amani 853. Holotype: B. Syn. of *C. mildbraedii*. Tanzania
Celtis utilis **(Caminhoá) Caminhoá**, Bot. Ger. Med. 5: 2237 (1883); Carauta, Rodriguésia 27, 39: 109 (1974).
Type: Basionym *Mertensia utilis* Caminhoá. Probably syn. of *Celtis orthocanthos*.
Celtis vandervoetiana **C.K.Schneid.** , Sarg. Pl. Wils. 3: 267 (1916).
Type: China: Szechuan, Veitch Exped. No 4467. BM, K. China (Szechuan).
Celtis velutina **Planch.**, Ann. Sci. Nat. Bot. sér. 3. 10: 313. (1848) & in Mart., Fl. Bras. 4(1): 1811 (1853).
Type: Peru, Quebrada de Pariahuanca, Mathews 826. Holotype: K, iso: K. Syn. of *C. iguanaea* (Jacq.) Sarg.
Celtis vesiculosa **Hochst. ex Planch.**, Ann. Sc. Nat. sér. 3, 10: 295. (1848).
Type: In mountibus Samensibus Abyssiniae, Schimper 1162, Ethiopia. Holotype: B?; iso: BM, K. Syn. of *C. kraussiana = C. africana*. Ethiopia, Tropical and S.Africa, Yemen).
Celtis villosula **Rydb.**, Fl. Rocky Mts. ed 2: 1116 (1923).
Type: Utah (without definite locality), M.E. Jones s.n. ILL, GH. USA.
Celtis virgata **Roxb.**, Wall. Cat. n. 3694 (1831).
Type: K-Wall. Syn. of *Trema timorensis*.
Celtis vitiensis **A.C.Smith**, Bull. Torrey Bot. Club 52: 536 (1943).
Type: Viti Levu: Tholo North: Vicinity of Nandarivatu, alt. 750 m, Nandrau, alt about 600 m.
Degener no 14322, Gillespie 4185. A, MO, B. Syn. of *C. paniculata* (Endl.) Planch. Pacific: Viti Levu: Tholo North: Vicinity of Nandarivatu.
Celtis waitzii **Blume**, Bot. Lugd. Bat. 2: 71 (1856).
Type: India, Bangladesh, Burma. Syn. of *C. cinnamomea* Lindl. Sri Lanka, India, Bangladesh, Burma, Thailand, Indo-China, Malaysia, Indonesia.
Celtis wallichii **Steud.**, Nom. ed. 2, 1: 316 (1840-41).
Nomen. East India. Syn. of *C. tetrandra*.
Celtis weddelliana **(Planch.) Romanczuk**, Hickenia, 1, 2: 8. (1976).
Type: Argentina.Corrientes: without locality, Feb 1832, Bonpland 1211. Lectotype: P. Syn. of *C. ehrenbergiana* (Klotsch) Liebm. Basionym: *C. tala* var. *weddelliana* Planch.
Celtis wightii **Planch.**, Ann. Sc. Nat. sér. 3, 10: 307 (1848).
Type: India, In peninsula Indiae orientalis, ibid in montibus Neelgherries Wight 85 & Wight s.n. & Ceylon, Walker 214 & Gardner s.n. (K). Syntypes: K. Accepted. India, Sri Lanka, S.E. Asia, Uganda, Kenya, Mozambique.
Celtis willdenowiana **Roem. & Schult.**, Syst. Veget. 6: 306 (1820).
Type: Japan. B. Syn. of *C. sinensis* var. *japonica*. Japan, China.
Celtis williamsii **Rusby**, Bull. N.Y. Bot. Gard. 6: 497 (1910).
Type: Bolivia: La Paz, San Buenaventura, 30 Nov 1901, R.S. Williams 603. Holotype: NY; iso: K, NY, US. Syn. of *C. iguanaea* (Jacq.) Sarg. Indian peninsula, Sri Lanka.
Celtis xizangensis **E.W.Ma**, Acta Phytotax. Sin. 18: 14 (1980).
Type: China: Tibet, Zhao Chong-fu 417. PE. China.
Celtis yangquanensis **E.W.Ma**, Bull. Lab. North- East. Forest. Inst. 1980, 7: 123 (1980).
Type: A, B, E, Hk. China.
Celtis yunnanensis **C.K.Schneid.** , Sarg. Pl. Wils. 3: 279 (1916).
Type: China: Yunnan, Collector: A. Henry 9323. Holotype: NY. China (Yunnan).
Celtis zenkeri **Engl.**, Notizbl. Bot. Gart. Berlin. 3: 22 (1900).
Type: Cameroon, Yaoundé, Zenker & Staudt 9. Holotype: B; iso: K, P. Accepted. Africa: Cameroun, Congo, RD Congo, Nigeria, Ghana, Cote d'Ivoire.

***Celtis zippelii* (Blume) Planch.**, in DC. Prodr. 17: 185 (1873).
Type: New Guinea, Zippel. Holotype: L. Basionym: *Solenostigma zippellii* Blume. Java. Close to *C. philippensis* Blanco s.s.
***Celtis zizyphoides* (Kunth) Spreng.**, Syst. Veg. 1: 932 (1824).
Type: Colombia: Bolivar, Rio Magdalena. Near Mompox (=Mompos), Michiqueo and Penones de Roso, May 1831, Humboldt s.n. Holotype (fragment): B; photograph in NY; iso: P, photograph in G. Basionym: *Mertensia ziziphoides* Kunth in Humb. & Bonpl., Nov. Gen.Sp. 2:26 (folio), 31 (quarto) (1817). Syn. of *C. iguanaea* (Jacq.) Sarg., other syn.: *Momisia ziziphoides* (Kunth) F.Dietr. New Grenada.

Chapter 10

SUMMARY AND CONCLUSIONS

A. SATTARIAN & L. J. G. VAN DER MAESEN

10.1 Introduction

Celtidaceae (formerly Ulmaceae-Celtidoideae) (Elias 1970; Grudzinskaya 1976; Judd et al. 1994; Omori et al. 1993, Omori & Terabayashi 1991, Ueda et al. 1997) comprise ca. 150 species classified in 9 genera. In Africa, Celtidaceae is a small family with the main genus *Celtis*.

The species, which are mostly trees, are found in tropical and temperate regions of the world. Some species of the family are ornamental; some are used for timber and reforestation. *Celtis* was reported to be represented by c. 8 species in tropical Africa (Letouzey 1972) but in current research 12 species can be distinguished (Sattarian & van der Maesen 2005). *Celtis* species range from North Africa (Algeria, Libya and Morocco) to South Africa and Madagascar.

The species are found in different ecological settings. Several tree species are found in the rain forest (*Celtis tessmannii, Celtis adolfi-friderici)*; some in semi-deciduous forest (*C. mildbraedii, C. prantlii, C. zenkeri*). Other *Celtis* are shrubs or small trees of rain forest undergrowth (*C. gomphophylla*), or found on the forest/savanna boundary, sometimes in mountain forest (*C. africana*). One species (*C. toka*) is a fairly large tree with a compact crown, living beside streams or planted in villages in the Sudano-Sahelian zone.

The main purpose of the research projects presented in this thesis was to identify the African *Celtis* species by different ways and means. Morphology and evolutionary relationships constitute the main chapters of the work.

In which family should *Celtis* be placed? Formerly it was classified in the Ulmaceae-Celtidoideae. A literature review formed the start of the work. As a first step in this research we looked at the history of this genus (its phylogeny and morphology).

10.2 Phylogeny

Molecular data show the place of Urticalean families within a well-defined and supported Rosales clade sensu APG 1998; including Barbeyaceae, Dirachmaceae, Eleagnaceae, Ramnaceae, and Rosaceae (Chase et al. 1993; Gunter, Kochert & Giannasi 1994; Soltis et al. 1997; Qiu et al. 1998). *Celtis, Humulus, Trema*, and *Boehmeria* are classified in an Urticalean clade with *Morus* and *Ficus,* and that Urticalean clade is placed in their Rosid I clade. The three-gene analysis of Soltis et al. (2000) also provided strong support for the separation of Ulmaceae and Celtidaceae. A small-scale *matk* analysis of Celtidaceae (5 genera of Celtidaceae and 8 other genera of Urticalean rosids) placed Cannabaceae solidly within a portion of the Celtidaceae (Song et al. 2001). Ulmaceae and Celtidaceae are separate families (Sytsma et al. 2002) while Cannabaceae and Celtidaceae should be merged. The origin of Cannabaceae within a clade of Celtidaceae is supported by ultrastructure, chromosome number, and cpDNA restriction site (Wiegrefe, Sytsma & Guries 1998) and matk data (Song et al. 2001) as well as with these *rbcL, trnL-F,* and *ndhF* sequence data. All the analyses of Sytsma et al. (2002) are based on *rbcL, trnL-F* and *ndhF*. *Gironniera* is sister to a clade comprising *Celtis*, *Chaetachme, Parasponia, Pteroceltis* and *Trema,* but these relationships are not well supported (Song et al. 2001).

10.3 Morphology

The family Ulmaceae Mirbel (sensu lato) consists of 15-19 genera and c. 150-200 species, depending on the authority quoted. Link (1831) was already of the opinion that the Ulmaceae had to be split into separate families: the Ulmaceae (*Ulmus* and related genera) and the Celtidaceae (*Celtis* and related genera). This proposal has not been generally been accepted since that time.

The Ulmaceae (Engler 1907) are divided in two subfamilies (Celtidoideae and Ulmoideae). Hutchinson (1976) divided the Ulmaceae genera in two tribes (Ulmeae and Celteae) according to the fruit type (fleshy fruits versus dry samara) and the major dispute appears to lie within the family. As Engler 1907 and Sweitzer 1971 indicated in their taxonomic reviews and anatomical studies of the family, the majority of morphological authorities considered the Ulmaceae to consist of two subfamilies; the Ulmoideae and the Celtidoideae (Engler 1907; Cronquist 1981, 1988; Sweitzer 1971).

Are the Ulmaceae a monophyletic group?

In Chapter 2, results clearly confirm that Ulmaceae s.1. is not a monophyletic group, and that the Celtidoids or Celtidaceae must be separated from it. Ulmaceae s.s. is sister to the other Urticalean Rosids, All the 125700 MP trees present the Celtidoids s.1. as sister to a clade with Moraceae and Urticaeae. Athough jackknife support for this relationship is only moderate (72% jackknife support) the high p.p. values (97 and 99) in the Bayesian analyses and congruence with the results of Sytsma et al. (2002) who acquired better support for this relationships with the addition of the chloroplast gene *ndhF*, indicate that support will probably increase with the addition of more character data.

Are the Celtidoid or Celtidaceae genera monophyletic?

Most Celtidaceae or Celtidoid genera are monophyletic; only the status of *Trema*, *Parasponia* and *Celtis* remains uncertain. It is clear that not all genera are represented by all their species, and the addition of more taxa could alter this conclusion.

What are the intergeneric relationships within the Celtidoids or Celtidaceae?

Aphananthe is sister to all other Celtidoid s.1. genera. *Lozanella* appears as sister to the remainder, and *Gironniera* as sister to a clade comprising *Celtis*, *Chaetachme*, *Parasponia*, *Pteroceltis*, and *Trema*, but these relationships are not well supported. It is possible that when more data is added, the positions of *Lozanella* and *Gironniera* would switch, or that both will appear as sister to each other.

Is African *Celtis* monophyletic within Celtidaceae?

The topology of the Jackknife analysis has shown a monophyletic clade of *Celtis* with 83% value support (*trnL-F*, morphology) and without morphology this clade received (64%) value support (fig. 3.1 &3.2). Generally *Celtis* appears in an unresolved clade containing *Pteroceltis*, *Trema*, *Chaetachme*, *Humulus* and *Cannabis* (99%). This clade is sister to *Gironniera* (67%), then to *Lozanella* (99%) and to *Aphananthe* (59%). The clade containing all Celtidaceae and Cannabaceae is related to *Ficus*, *Brosimimum*, *Morus*, *Cecropia*, *Pellionia* (100%) and finally sister to *Ampelocera*, and *Ulmus* (100%). In general this topology shows that genera of Celtidaceae are monophyletic. In the *Celtis* clade *Celtis gomphophylla* is sister to all other *Celtis*. South American taxa form a clade of their own (81%).

The Sub-clade and other African and Asian taxa are placed together and display no special pattern, in this clade a polytomy is seen, which means that for better-resolved patterns different markers are needed as well as more taxa.

Is there any relationship between phylogeny and biogeography?

African and Asian taxa are together and display no special pattern, in this clade a polytomy is seen, but there is a pattern for South American *Celtis* that can morphologically be distinguished by the presence of thorns (figs 3.1 & 3.2). There is no clade for African and Asian species of *Celtis,* this means that they are paraphyletic according to *trnL-F* marker. Geographical distribution, except for South American species, does not provide specific patterns. We need better DNA sequence markers for a better-resolved phylogeny.

Which are useful macro- and micro-morphological characters?

Celtis is a widespread tree genus, its species can be small in size; from 4m tall in *Celtis africana* to 40 m tall for *Celtis tessmannii*. *Celtis* trunks vary from cylindrical and sub-cylindrical with branches in the crown, to branched at lower levels. In tropical *Celtis* species normally cylindrical stems are seen e.g. in *C. adolfi-friderici,* and *C. tessmanni.* The bark in African *Celtis* is smooth and whitish to grey; buttresses are present in *C. adolfi-friderici*, and *C. tessmanni. Celtis* yields a lightweight to heavy hard wood with a density of 400-960 kg/m$^{3.}$

In African *Celtis* different types of hairs can be distinguished, glandular and non-glandular ones, with various densities of hairs on leaves, or other parts of trees. Leaf shapes range from ovate to lancolate.

In African *Celtis* the pattern of stomata in epidermis is useful. A paracytic pattern is found in *Celtis africana, C. tessmannii, C. mildbraedii, C. zenkeri, C. prantlii,* and *C. bifida.* Anisocytic stomata are seen in *Celtis adolfi-friderici, C. toka* and cyclocytic stomata are found in *Celtis gomphophylla*, and *C. africana*. Inflorescences in *Celtis* are cymose or fasciculate. In general *Celtis* pollen is not very variable. It is triporate, spheroidal and small- to medium-sized. Most of the species show a sunken area around the pore in SEM (not in LM).This area is never present in pollen grains of *C. africana* and *C. gomphophylla*. According to the P/E ratio and size a distinction can be made between Asian and African *Celtis* species (see Fig. 5.2): pollen grains of Asian *Celtis* species *(Celtis occidentalis, C. sinensis, C. tournefortii)* are bigger and more oblate than those of African species. Furthermore, among African species the tropical species (*C. tessmannii*, *C. adolfi-friderici*) have smaller pollen than the species from drier areas (*C. africana*, *C. gomphophylla).* Morphology of African *Celtis* species do not seem to be correlated with other taxonomic characters.

The drupaceous fruits of the *Celtis* vary in colour from bright yellow to orange, deep red, and purple and are primarily bird-dispersed water dispersal occurs as well. Endocarp characters prove to be important to distinguish species of African *Celtis* in Ulmaceae/Celtidaceae.

The endocarp shape varies from elliptic to ovoid, lenticular, or ovoid-beaked. The size of endocarp ranges from small (4 x 3 x 2 mm) to large (11 x 10x 8) and is very useful in terms of identification of species. The endocarp colour varies from white, cream, and grey to brown and helps to separate species. The endocarp shape varies from globular to polygonal. The outer layers of the endocarp differ; they curve, and are raised from the bottom to the top but in different directions. The apex of the endocarp is round or beaked. The ridges of the endocarp are another character; from a faint ridge to 1--3 clear ridges can be seen among African *Celtis*. Outer layers of the endocarp (sculpture) vary from smooth with different size of holes, to a prominent rough surface, and membranous platelets can be present. The ratio of D/L endocarp length also varies from ¾ to 6/8,

African *Celtis* species often have a polygonal sculpture. This structure is formed by the ridges and cross-connection between the edges. Polygonal sculpture is found in *Celtis adolfi-friderici, C. africana, C. australis, C. toka, C. tessmannii, C. bifida,* and *C. mildbraedii,* and normally the surface is rough, especially in *C. tessmannii* and *C. adolfi-friderici,* and the polygones are curved. A non-polygonal shape is found in *C. gomphophylla*, but there are some prominent edges from the bottom. *C. philippensis* s.s. has also a non-polygonal shape and smooth surface. In some species the apex is conspicuously pitted: in *C. adolfi -friderici*, *C. gomphophylla,* and *C. tessmannii.*

With high magnification the outer walls of the endocarp or periclinal walls can be seen to differ. There are two main types. One type of endocarp has rough layers with different sizes of holes, prominent sculpturing, and membranous platelets, while the other one is smooth-layered and fissured, it looks like films in different layers, smooth layers and crusts, and the coverings are usually continuous without very prominent surface sculpturing.

10.4 Conclusions

- Ulmaceae s.1. is not a monophyletic group, and the Celtidoids or Celtidaceae must be separated from it.
- Most Celtidaceae or Celtidoid genera are monophyletic; only the status of *Trema*, *Parasponia* and *Celtis* remains uncertain.
- African *Celtis* is not a monophyletic group.
- Geographical distribution, except for South American species, does not provide specific phylogenetic patterns. We need better DNA sequence markers for a better-resolved phyloeny.
- The endocarp character was discerned as new and important in African *Celtis*. The shape of the endocarp showed variation among the African C*eltis*.
- Description of the pollen grains of all African *Celtis* species was provided.
- African *Celtis* was taxonomically revised, resulting in the distinction of 12 species for that continent.
- Two new species have been described: *Celtis australiensis* Sattarian is described from Australia, and *Celtis malagasica* Sattarian is new for Madagascar.

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Appendix 1.

Taxon list with information on used markers and codes. Source information is given for new sequences (herbarium or botanic garden). Successful amplifications are indicated by a Y under the concerned marker (*rbcL1, rbcL2, trnL, trnL-F*). Missing data are indicated by hyphens. Two species of *Crataegus* (Rosaceae) are combined in the dataset.

Family	**Genus**	**Species**	***rbcL1***	***rbcL2***	***trnL***	***trnL-F***	**Code**	**Source**	**Source/code**	**Collector**	**Number.**
Barbeyaceae	*Barbeya*	*oleoides*	AJ225788		AJ225795		AJ225788	GenBank			
Cannabaceae	*Cannabis*	*Sativa 1*	AF500344		AF501598		AF500344	GenBank			
	Cannabis	*Sativa 2*	AJ390068		AJ390367		AJ390068	GenBank			
	Humulus	*japonicus*	Y	-	Y	Y	Hujap36	U	U0034889	Windler, D.	4046
	Humulus	*lupulus*	AF061992		AF501599		AF061992	GenBank			
Cecropiaceae	*Cecropia*	*palmata*	AF061196		AF501615		AF061196	GenBank			
	Coussapoa	*ovalifolia*	-	-	AF501616		AF501616	GenBank			
Celtidaceae	*Aphananthe*	*aspera*	AF500339		AF501594		AF500339	GenBank			
	Aphananthe	*monoica*	Y	-	Y	Y	Apmon35	U	U0034883	Fernández N, R.	3462
	Aphananthe	*philippensis 1*	Y	-	Y	Y	Apphi64	L	L0413100	Forster, P.I.	6657
	Aphananthe	*philippensis 2*	-	-	Y	Y	Apphi96	L	L0413099	Mabberley, D.J.	1785
	Celtis	*aetnensis*	Y	Y	Y	Y	Ceaet52	Catania B.G.			
	Celtis	*africana*	Y	Y	Y	Y	Ceafr32	BR		Wellas, N.J.	2717
	Celtis	*australiensis*	Y	Y	-	-	CeausA4	L		Forbes, S.J.	389
	Celtis	*australis*	Y	Y	Y	Y	Ceaus51	Wageningen B.G.	BG07840	Sattarian, A.	22
	Celtis	*brasiliensis*	Y	-	Y	Y	Cebra33	U		Simonis, J.E.	165
	Celtis	*caucasica*	Y	-	Y	Y	Cecau07	Utrecht B.G	81RD00394	Velzen, R. van	12
	Celtis	*durandii*	Y	Y	Y	Y	Cedur66	Meise B.G	19620209		
	Celtis	*Edulis*	Y	Y	Y	Y	Ceedu59	Kew B.G	1982-8477	Chase, M.	20136
	Celtis	*ehrenbergiana*	-	-	Y	-	CeehrA3	U		Stephental	4435
	Celtis	*gomphophylla*	Y	Y	Y	Y	Cegom25	CO		Hafashimana	177
	Celtis	*iguanaea 1*	-	-	AY488673		AY488673	GenBank			
	Celtis	*iguanaea 2*	Y	Y	Y	Y	Ceigu69	U		Nee, M.	26592
	Celtis	*julianae*	Y	Y	Y	Y	Cejul48	Mt Holyoke B.G.	990600-1		
	Celtis	*koraiensis*	Y	Y	Y	Y	Cekor11	U	84RD00179	Velzen, R. van	13
	Celtis	*laevigata*	Y	Y	Y	Y	Celae45	Wageningen B.G	BG22927	Sattarian, A.	25
	Celtis	*malagasica*	Y	Y	Y	Y	Cemad68	MO			2993
	Celtis	*mildbraedii*	Y	Y	Y	Y	Cemil31	WAG	148228	s.n.	1138
	Celtis	*occidentalis*	Y	Y	Y	Y	Ceocc54	Mt Holyoke B.G	970126-1		
	Celtis	*selloviana*	Y	Y	Y	Y	Cesel16	Wageningen B.G	85BG07007	Leeuw, H. de	421
	Celtis	*sinensis*	Y	Y	Y	Y	Cesin47	Helsinki B.G	2003-0564		

Family	**Genus**	**Species**	***rbcL1***	***rbcL2***	***trnL***	***trnL-F***	**Code**	**Source**	**Source/code**	**Collector**	**Number.**
	Celtis	*sinensis* japonica	D86309		-	-	D86309	GenBank			
	Celtis	*Tala*	Y	Y	Y	Y	Cetal67	Meise B.G	19371993		
	Celtis	*tournefortii*	Y	Y	Y	Y	Cetou17	Wageningen B.G	80BG45421	Leeuw, H. de	452
	Celtis	*zenkeri*	Y	Y	Y	Y	Cezen30	WAG	149438	s.n.	1768
	Chaetachme	*aristata 1*	Y	Y	Y	Y	Chari41	L	L0413098	Schijff, H.P. v.d.	3444
	Chaetachme	*aristata 2*	D86310		-	-	D86310	GenBank			
	Chaetachme	*madagascariensis*	Y	Y	Y	Y	Chmad94	WAG		McPherson, G	14423
	Chaetachme	*microcarpa*	Y	Y	-	-	Chmic92	WAG		Bamps, P	4325
	Gironniera	*celtidifolia*	Y	Y	Y	-	Gicel103	L	L0413097	Sands, M.J.S.	855
	Gironniera	*Hirta*	Y	-	Y	Y	Gihir76	L	L0413094	Hoogland, R.D.	10351
	Gironniera	*rhamnifolia*	-	-	Y	Y	Girha77	L	L0413090	Hoogland, R.D.	10541
	Gironniera	*subaequalis 1*	AF500340		-	-	AF50034	GenBank			
	Gironniera	*subaequalis 2*	D86311		-	-	D86311	GenBank			
	Gironniera	*subaequalis 3*	Y16772		-	-	Y16772	GenBank			
	Lozanella	*enantiophylla*	AF500341		AF501595		AF5003	GenBank			
	Lozanella	*permollis*	Y	-	Y	Y	Loper38	U	U034890	Solomon, J.C.	18073
	Lozanella	*trematoides*	Y	Y	Y	Y	Lotre71	L	L0413085	Pringle, C.G.	8983
	Parasponia	*andersonii*	Y	Y	Y	Y	Paand65	L		Meyer, J.-Y.	2556
	Parasponia	*melastomatifolia*	Y	Y	Y	Y	Pamel72	L	L0413079	Pullen, R.	7963
	Parasponia	*parviflora*	AF500342		AF501596		AF500342	GenBank			
	Parasponia	*Rigida 1*	-	-	AY488675		AY488675	GenBank			
	Parasponia	*Rigida 2*	U59820		-	-	U59820	GenBank			
	Parasponia	*rugosa*	-	-	Y	Y	Parug74	L	L0413074	Damas, K.	74501
	Parasponia	*simulans*	-	-	AY488674		AY488674	GenBank			
	Pteroceltis	*tatarinowii*	AF500343		AF501597		AF5003	GenBank			
	Trema	*africana*	-	-	AY488690		AY488690	GenBank			
	Trema	*aspera*	-	-	AY488681		AY488681	GenBank			
	Trema	*cannabina*	Y	Y	Y	Y	Trcan81	Hawaii B.G	980151	Lorence, D.	9381
	Trema	*cannabina* dielsiana	-	-	AY488678		AY488678	GenBank			
	Trema	*discolor*	Y	Y	Y	Y	Trdis80	Hawaii B.G		Lorence, D.	9329
	Trema	*domingense*	Y	Y	Y	Y	Trdom44	U	U034891	Ekman, E.L.	12293
	Trema	*integerrima*	-	-	AY488716		AY488716	GenBank			
	Trema	*lamarckiana*	-	-	AY488696		AY488696	GenBank			
	Trema	*micrantha 1*	Y	Y	Y	Y	Trmic12	U		Chatrou, L.W.	413
	Trema	*micrantha 2*	U03844		-	-	U03844	GenBank			
	Trema	*nitens*	-	-	AY488679		AY488679	GenBank			
	Trema	*orientalis*	D86313		-	-	D86313	GenBank			
	Trema	*orientalis I*	-	-	AY488688		AY488688	GenBank			

Family	**Genus**	**Species**	***rbcL1***	***rbcL2***	***trnL***	***trnL-F***	**Code**	**Source**	**Source/code**	**Collector**	**Number.**
	Trema	*orientalis II*	-	-	AY488693		AY488693	GenBank			
	Trema	*politoria*	-	-	AY488677		AY488677	GenBank			
	Trema	*tomentosa*	-	-	AY488685		AY488685	GenBank			
	Trema	*virgata*	-	-	AY488683		AY488683	GenBank			
Dirachmaceae	*Dirachma*	*socotrana*	AJ225789		AJ225796		AJ225789	GenBank			
Elaeagnaceae	*Elaeagnus*	*angustifolia*	U17038		Y	-	U17038	GenBank			
	Shepherdia	*argentea*	AJ225787		AJ225794		AJ225787	GenBank			
Moraceae	*Artocarpus*	*Altilis*	AF500345		AF501600		AF500345	GenBank			
	Brosimum	*alicastrum*	AF500346		AF501601		AF500346	GenBank			
	Broussonetia	*papyrifera*	AF500347		AF501602		AF5003	GenBank			
	Castilla	*elastica*	AF500348		AF501603		AF500348	GenBank			
	Dorstenia	*mannii*	AF500349		AF501604		AF500349	GenBank			
	Ficus	*benjamina*	AF500350		AF501605		AF500350	GenBank			
	Ficus	*pumila*	AF500352		AF501606		AF500352	GenBank			
	Maclura	*cochinchinensis*	-	-	AF501607		AF5016	GenBank			
	Maclura	*pomifera*	D86318		-	-	D86318	GenBank			
	Morus	*Alba*	D86319		AF501608		D86319	GenBank			
	Streblus	*pendulinus*	AF500353		AF501609		AF500353	GenBank			
Rhamnaceae	*Berchemia*	*discolor*	AJ225786		AJ225793		AJ225786	GenBank			
	Ceanothus	*coeruleus*	-	-	AJ225798		AJ225798	GenBank			
	Ceanothus	*sanguineus*	U06795		-	-	U06795	GenBank			
	Colletia	*ulcinia*	U59819		AY460412		U59819	GenBank			
	Discaria	*chacaye*	U59826		AY460415		U59826	GenBank			
	Hippophae	*salicifolia*	U59821		AJ225801		U59821	GenBank			
	Nesiota	*elliptica*	AJ225783		AJ225803		AJ225783	GenBank			
	Phylica	*polifolia*	AJ225784		AJ226791		AJ225784	GenBank			
	Rhamnus	*lycioides*	AJ390070		AJ225790		AJ390070	GenBank			
	Zizyphus	*aff. glabrata*	U60313		AJ225799		U60313	GenBank			
Rosaceae	*Aruncus*	*dioicus*	U06794		AF348536		U06794	GenBank			
	Crataegus	*Columbiana (rbcL)* *monogyna (trnL-F)*	U06799		AF348541		U06799	GenBank			
	Dryas	*drummondii*	U59818		AJ225802		U59818	GenBank			
	Geum	*chiloense*	L01921		-	-	L01921	GenBank			
	Potentilla	*fruticosa*	U06818		AF348557		U06818	GenBank			
	Prunus	*emarginata*	U06820		AF318670		U06820	GenBank			
	Rosa	*woodsii*	U06824		-	-	U06824	GenBank			
Ulmaceae	*Ampelocera*	*hottleyi*	AF500335		AF501592		AF500335	GenBank			
	Hemiptelea	*davidii*	AF500336		-	-	AF500336	GenBank			

Family	**Genus**	**Species**	***rbcL1***	***rbcL2***	***trnL***	***trnL-F***	**Code**	**Source**	**Source/code**	**Collector**	**Number.**
	Holoptelea	*integrifolia*	D86315		-	-	D86315	GenBank			
	Ulmus	*americana*	AF500337		AF501593		AF500337	GenBank			
	Zelkova	*serrata 1*	Y	Y	Y	Y	Zeser05	Utrecht B.G	92RD00266	Velzen, R. van	9
	Zelkova	*serrata 2*	AF500338		-	-	AF500338	GenBank			
Urticaceae	*Boehmeria*	*calophleba*	AY208700		AY208723		AY208700	GenBank			
	Boehmeria	*Nivea*	AF062005		AF501610		AF062005	GenBank			
	Elatostema	*parvum*	AY208703		AY208733		AY208703	GenBank			
	Hesperocnide	*tenella*	AF500355		-	-	AF500355	GenBank			
	Laportea	*canadensis*	AF500356		-	-	AF500356	GenBank			
	Myriocarpa	*longipes*	AY208705		AY208724		AY208705	GenBank			
	Parietaria	*pensylvanica*	AF500357		AF501611		AF5003	GenBank			
	Pellionia	*daveauana*	AF500358		AF501612		AF500358	GenBank			
	Pilea	*depressa*	AF500359		AF501613		AF500359	GenBank			
	Pilea	*nummulariifolia*	-	-	AY208727		AY208727	GenBank			
	Poikilospermum	*sp. Wooliams 54*	AF500362		AF501617		AF500362	GenBank			
	Procris	*frutescens*	Y	Y	AY208704		AY208704	GenBank			
	Urera	*glabra*	AF500360		AF501614		AF500360	GenBank			
	Urtica	*Dioica*	AY208707		AY208725		AY208707	GenBank			
Betulaceae	*Alnus*	*incana*	X56618		AF327574		X56618	GenBank			
Betulaceae	*Betula*	*papyrifera*	X56617		-	-	X56617	GenBank			
Casuarinaceae	*Casuarina*	*equisetifolia*	AY033859		AY147090		AY0338	GenBank			
Fagaceae	*Castanea*	*crenata*	AB060565		AF344181		AB060565	GenBank			
Fagaceae	*Fagus*	*sylvatica*	L13340		AF133654		L13340	GenBank			
Juglandaceae	*Carya*	*glabra*	Y	Y	L12637		L12637	GenBank			
Juglandaceae	*Juglans*	*Nigra*	AF206785		AY231170		AF206785	GenBank			
Myricaceae	*Morella*	*cerifera*	AJ626759		AY147093		AJ626759	GenBank			
Myricaceae	*Myrica*	*Gale*	AJ626757		-	-	AJ626757	GenBank			
Nothofagaceae	*Nothofagus*	*antarctica*	L13343		AY147091		L13343	GenBank			

Appendix 2

Taxon list with morphological characters, Unisexual, Hermaphrodite, Male (U/H/H+M).

Family	**Genus**	**Species**	**Habit**	**Leaf arr.**	**Flowering Habit**	**Flowers**	**Fruit type**	**Leaf margin**	**Pollen type**	**Thorns**
Barbeyaceae	*Barbeya*	*oleoides*	Tree	opposite	dioecious	U	Achene	entire	3 porate	absent
Cannabaceae	*Cannabis*	*sativa 1*	Herb	alternate	dioecious	U	Achene	lobed	3 porate	absent
	Cannabis	*sativa 2*	Herb	alternate	dioecious	U	Achene	lobed	3 porate	absent
	Humulus	*japonicus*	Herb	alternate	dioecious	U	Achene	lobed	3 porate	absent
	Humulus	*lupulus*	Herb	alternate	dioecious	U	Achene	lobed	3 porate	absent
Cecropiaceae	*Cecropia*	*palmata*	Tree	alternate	monoecious	U	Achene	lobed	<3 porate	absent
	Coussapoa	*ovalifolia*	Tree	alternate	monoecious	H	Drupe	entire	<3 porate	absent
Celtidaceae	*Aphananthe*	*aspera*	Tree	alternate	monoecious	H	Drupe	entire	3 porate	absent
	Aphananthe	*monoica*	Tree	alternate	monoecious	H	Drupe	entire	3 porate	absent
	Aphananthe	*philippensis 1*	Tree	alternate	monoecious	H	Drupe	entire	3 porate	absent
	Aphananthe	*philippensis 2*	Tree	alternate	monoecious	H	Drupe	entire	3 porate	absent
	Celtis	*aetnensis*	Tree	alternate	monocious	H+M	Drupe	serrate	3 porate	absent
	Celtis	*africana*	Tree	alternate	monocious	H+M	Drupe	serrate	3 porate	absent
	Celtis	*australiensis*	Tree	alternate	monocious	H+M	Drupe	entire	3 porate	absent
	Celtis	*australis*	Tree	alternate	monocious	H+M	Drupe	serrate	3 porate	absent
	Celtis	*brasiliensis*	Tree	alternate	monocious	H+M	Drupe	serrate	3 porate	thorns
	Celtis	*caucasica*	Tree	alternate	monocious	H+M	Drupe	serrate	3 porate	absent
	Celtis	*durandii*	Tree	alternate	monocious	H+M	Drupe	entire	3 porate	absent
	Celtis	*edulis*	Tree	alternate	monocious	H+M	Drupe	entire	3 porate	absent
	Celtis	*ehrenbergiana*	Tree	alternate	monocious	H+M	Drupe	?	3 porate	thorns
	Celtis	*gomphophylla*	Tree	alternate	monocious	H+M	Drupe	entire	3 porate	absent
	Celtis	*iguanaea 1*	Tree	alternate	monocious	H+M	Drupe	?	3 porate	thorns
	Celtis	*iguanaea 2*	Tree	alternate	monocious	H+M	Drupe	?	3 porate	thorns
	Celtis	*julianae*	Tree	alternate	monocious	H+M	Drupe	?	3 porate	absent
	Celtis	*koraiensis*	Tree	alternate	monocious	H+M	Drupe	serrate	3 porate	absent
	Celtis	*laevigata*	Tree	alternate	monocious	H+M	Drupe	serrate	3 porate	absent
	Celtis	*malagasica*	Tree	alternate	monocious	H+M	Drupe	entire	3 porate	absent
	Celtis	*mildbraedii*	Tree	alternate	monocious	H+M	Drupe	entire / serrate	3 porate	absent
	Celtis	*occidentalis*	Tree	alternate	monocious	H+M	Drupe	serrate	3 porate	absent
	Celtis	*selloviana*	Tree	alternate	monocious	H+M	Drupe	serrate	3 porate	absent
	Celtis	*sinensis*	Tree	alternate	monocious	H+M	Drupe	serrate	3 porate	absent
	Celtis	*sinensis* japonica	Tree	alternate	monocious	H+M	Drupe	serrate	3 porate	absent
	Celtis	*tala*	Tree	alternate	monocious	H+M	Drupe	serrate	3 porate	thorns

Family	Genus	Species	Habit	Leaf arr.	Flowering Habit	Flowers	Fruit type	Leaf margin	Pollen type	Thorns
	Celtis	*tournefortii*	Tree	alternate	monocious	H+M	Drupe	serrate	3 porate	absent
	Celtis	*zenkeri*	Tree	alternate	monocious	H+M	Drupe	entire / serrate	3 porate	absent
	Chaetachme	*aristata 1*	Tree	alternate	monoecious	H	Drupe	entire	3 porate	thorns
	Chaetachme	*aristata 2*	Tree	alternate	monoecious	H	Drupe	entire	3 porate	thorns
	Chaetachme	*madagascariensis*	Tree	alternate	monoecious	H	Drupe	entire	3 porate	thorns
	Chaetachme	*microcarpa*	Tree	alternate	monoecious	H	Drupe	entire	3 porate	thorns
	Gironniera	*celtidifolia*	Tree	alternate	monoecious	H	Drupe	serrate	3 porate	absent
	Gironniera	*hirta*	Tree	alternate	monoecious	H	Drupe	serrate	3 porate	absent
	Gironniera	*rhamnifolia*	Tree	alternate	monoecious	H	Drupe	serrate	3 porate	absent
	Gironniera	*subaequalis 1*	Tree	alternate	monoecious	H	Drupe	serrate	3 porate	absent
	Gironniera	*subaequalis 2*	Tree	alternate	monoecious	H	Drupe	serrate	3 porate	absent
	Gironniera	*subaequalis 3*	Tree	alternate	monoecious	H	Drupe	serrate	3 porate	absent
	Lozanella	*enantiophylla*	Tree	opposite	dioecious	U	Drupe	serrate	3 porate	absent
	Lozanella	*permollis*	Tree	opposite	dioecious	U	Drupe	serrate	3 porate	absent
	Lozanella	*trematoides*	Tree	opposite	dioecious	U	Drupe	serrate	3 porate	absent
	Parasponia	*andersonii*	Tree	alternate	monoecious	H	Drupe	serrate	3 porate	absent
	Parasponia	*melastomatifolia*	Tree	alternate	monoecious	H	Drupe	serrate	3 porate	absent
	Parasponia	*parviflora*	Tree	alternate	monoecious	H	Drupe	serrate	3 porate	absent
	Parasponia	*rigida 1*	Tree	alternate	monoecious	H	Drupe	serrate	3 porate	absent
	Parasponia	*rigida 2*	Tree	alternate	monoecious	H	Drupe	serrate	3 porate	absent
	Parasponia	*rugosa*	Tree	alternate	monoecious	H	Drupe	serrate	3 porate	absent
	Parasponia	*simulans*	Tree	alternate	monoecious	H	Drupe	serrate	3 porate	absent
	Pteroceltis	*tatarinowii*	Tree	alternate	monoecious	H	Drupe	serrate	3 porate	absent
	Trema	*africana*	Tree	alternate	monoecious	H	Drupe	serrate	<3 porate	absent
	Trema	*aspera*	Tree	alternate	monoecious	H	Drupe	serrate	<3 porate	absent
	Trema	*cannabina*	Tree	alternate	monoecious	H	Drupe	serrate	<3 porate	absent
	Trema	*cannabina* dielsiana	Tree	alternate	monoecious	H	Drupe	serrate	<3 porate	absent
	Trema	*discolor*	Tree	alternate	monoecious	H	Drupe	serrate	<3 porate	absent
	Trema	*domingense*	Tree	alternate	monoecious	H	Drupe	serrate	<3 porate	absent
	Trema	*integerrima*	Tree	alternate	monoecious	H	Drupe	serrate	<3 porate	absent
	Trema	*lamarckiana*	Tree	alternate	monoecious	H	Drupe	serrate	<3 porate	absent
	Trema	*micrantha 1*	Tree	alternate	monoecious	H	Drupe	serrate	<3 porate	absent
	Trema	*micrantha 2*	Tree	alternate	monoecious	H	Drupe	serrate	<3 porate	absent
	Trema	*nitens*	Tree	alternate	monoecious	H	Drupe	serrate	<3 porate	absent
	Trema	*orientalis*	Tree	alternate	monoecious	H	Drupe	serrate	<3 porate	absent
	Trema	*orientalis I*	Tree	alternate	monoecious	H	Drupe	serrate	<3 porate	absent
	Trema	*orientalis II*	Tree	alternate	monoecious	H	Drupe	serrate	<3 porate	absent
	Trema	*politoria*	Tree	alternate	monoecious	H	Drupe	serrate	<3 porate	absent

Family	Genus	Species	Habit	Leaf arr.	Flowering Habit	Flowers	Fruit type	Leaf margin	Pollen type	Thorns
	Trema	*tomentosa*	Tree	alternate	monoecious	H	Drupe	serrate	<3 porate	absent
	Trema	*virgata*	Tree	alternate	monoecious	H	Drupe	serrate	<3 porate	absent
Dirachmaceae	*Dirachma*	*socotrana*	Shrub	alternate	monoecious	H	Capsule	serrate	?	absent
Elaeagnaceae	*Elaeagnus*	*angustifolia*	Tree	alternate	dioecious	U	Drupe	entire	3 porate	thorns
	Shepherdia	*argentea*	Shrub	opposite	monoecious	H	Drupe	serrate	?	thorns
Moraceae	*Artocarpus*	*altilis*	Tree	alternate	monoecious	H	Syncarp	serrate	3 porate	absent
	Brosimum	*alicastrum*	Tree	alternate	monoecious	H	Syncarp	entire	?	absent
	Broussonetia	*papyrifera*	Tree	alternate	monoecious	H	Syncarp	entire	?	absent
	Castilla	*elastica*	Tree	alternate	monoecious	H	Drupe	?	?	absent
	Dorstenia	*mannii*	Shrub	alternate	monoecious	H	Drupe	entire	>3porate	absent
	Ficus	*benjamina*	Tree	alternate	monoecious	H	Syncarp	entire / lobed	<3 porate	absent
	Ficus	*pumila*	Tree	alternate	monoecious	H	Syncarp	entire / lobed	<3 porate	absent
	Maclura	*cochinchinensis*	Tree	alternate	dioecious	U	Syncarp	?	?	absent
	Maclura	*pomifera*	Tree	alternate	dioecious	U	Syncarp	?	?	absent
	Morus	*alba*	Tree	alternate	monoecious	H	Syncarp	entire / lobed	3 porate	absent
	Streblus	*pendulinus*	Tree	opposite	monoecious	H	Drupe	serrate	?	absent
Rhamnaceae	*Berchemia*	*discolor*	Shrub	alternate	dioecious	U	Drupe	?	>3porate	absent
	Ceanothus	*coeruleus*	Shrub	alternate	monoecious	H	Capsule	entire	?	absent
	Ceanothus	*sanguineus*	Shrub	alternate	monoecious	H	Capsule	entire	?	absent
	Colletia	*ulcinia*	Shrub	alternate	monoecious	H	Capsule	entire	3 porate	absent
	Discaria	*chacaye*	Shrub	alternate	monoecious	H	Capsule	?	3 porate	absent
	Hippophae	*salicifolia*	Tree	alternate	dioecious	U	?	?	>3porate	thorns
	Nesiota	*elliptica*	Tree	opposite	monoecious	H	?	?	?	absent
	Phylica	*polifolia*	Shrub	alternate	monoecious	H	?	?	3 porate	absent
	Rhamnus	*lycioides*	Tree	alternate	monoecious	H	Drupe	serrate	?	absent
	Zizyphus	*aff. glabrata*	Tree	alternate	monoecious	H	Drupe	serrate	3 porate	absent
Rosaceae	*Aruncus*	*dioicus*	Herb	alternate	dioecious	H	Follicle	serrate	3 porate	absent
	Crataegus	*Columbiana monogyna)*	Shrub	alternate	monoecious	H	?	serrate	3 porate	absent
	Dryas	*drummondii*	Shrub	alternate	monoecious	H	Achene	entire	?	absent
	Geum	*chiloense*	Herb	alternate	monoecious	H	Achene	serrate	3 porate	absent
	Potentilla	*fruticosa*	Herb	alternate	monoecious	H	Achene	serrate	3 porate	absent
	Prunus	*emarginata*	Tree	alternate	monoecious	H	Drupe	entire	3 porate	absent
	Rosa	*woodsii*	Shrub	alternate	monoecious		Achene	serrate	3 porate	spines
Ulmaceae	*Ampelocera*	*hottleyi*	Tree	alternate	monoecious	H	Drupe	entire	>3porate	absent
	Hemiptelea	*davidii*	Tree	alternate	dioecious	U	Samara	serrate	>3porate	thorns
	Holoptelea	*integrifolia*	Tree	alternate	monocious	H	Samara	entire	>3porate	absent
	Ulmus	*americana*	Tree	alternate	monoecious	H	Samara	serrate	>3porate	absent

Family	**Genus**	**Species**	**Habit**	**Leaf arr.**	**Flowering Habit**	**Flowers**	**Fruit type**	**Leaf margin**	**Pollen type**	**Thorns**
	Zelkova	*serrata 1*	Tree	alternate	monoecious	H	Drupe	serrate	>3porate	absent
	Zelkova	*serrata 2*	Tree	alternate	monoecious	H	Drupe	serrate	>3porate	absent
Urticaceae	*Boehmeria*	*calophleba*	Shrub	alternate	monoecious	H	Achene	serrate	3 porate	absent
	Boehmeria	*nivea*	Shrub	alternate	monoecious	H	Achene	serrate	3 porate	absent
	Elatostema	*parvum*	Herb	alternate	monoecious	H	Achene	?	3 porate	absent
	Hesperocnide	*tenella*	Herb	opposite	monoecious	H	Achene	?	?	absent
	Laportea	*canadensis*	Herb	alternate	monoecious	H	Achene	?	>3porate	absent
	Myriocarpa	*longipes*	Shrub	alternate	dioecious	U	Achene	serrate	?	absent
	Parietaria	*pensylvanica*	Herb	alternate	monoecious	H	Achene	?	3 porate	absent
	Pellionia	*daveauana*	Herb	alternate	monoecious	H	Achene	entire	>3porate	absent
	Pilea	*depressa*	Shrub	opposite	monoecious	H	Achene	entire	>3porate	absent
	Pilea	*nummulariifolia*	Shrub	opposite	monoecious	H	Achene	entire	>3porate	absent
	Poikilospermum	*sp. Wooliams 54*	Herb	alternate	monoecious	H	Achene	entire	?	absent
	Procris	*frutescens*	Shrub	alternate	monoecious	H	Achene	entire	?	absent
	Urera	*glabra*	Shrub	alternate	monoecious	H	Achene	entire	>3porate	absent
	Urtica	*dioica*	Herb	opposite	monoecious	H	Achene	serrate	3 porate	absent
Betulaceae	*Alnus*	*incana*	Tree	alternate	dioecious	U	Achene	entire / serrate	?	absent
Betulaceae	*Betula*	*papyrifera*	Tree	alternate	dioecious	U	Achene	serrate	3 porate	absent
Casuarinaceae	*Casuarina*	*equisetifolia*	Tree	alternate	dioecious	U	Drupe	serrate	3 porate	absent
Fagaceae	*Castanea*	*crenata*	Tree	alternate	dioecious	U	Achene	serrate	?	absent
Fagaceae	*Fagus*	*sylvatica*	Shrub	alternate	monoecious	H	Samara	serrate	3 porate	absent
Juglandaceae	*Carya*	*glabra*	Tree	alternate	dioecious	U	Achene	entire	3 porate	absent
Juglandaceae	*Juglans*	*nigra*	Tree	alternate	dioecious	U	Drupe	entire	3 porate	absent
Myricaceae	*Morella*	*cerifera*	?	alternate	?	?	Syncarp	?	?	absent
Myricaceae	*Myrica*	*gale*	Shrub	alternate	monoecious	H	?	serrate	?	absent
Nothofagaceae	*Nothofagus*	*antarctica*	Tree	alternate	monoecious	H	Achene	serrate	3 porate	absent

Appendix 3

Taxon list with Extraction number, Species, Collection or Gen Bank no, Herbarium, Herbarium or Silicagel material (H/S), Origin. All material has marker *trnL-F*.

Extr. nr	**Species**	**Collection or Gen Bank no.**	**Herb.**	**H/S**	**Origin**
5	*Celtis adolfi-friderici* Celtidaceae	V.J. Jakiaje 842	MO	H	Cameroon
52	*C. aetnensis* Celtidaceae	Catania bot gard, Sicily		S	Italy
32, 58	*C. africana* Celtidaceae	M.J. Wells 2717	WAG	H	South Africa
136	*C. australiensis* Celtidaceae	S.J. Forbes 1997	CANB	H	Australia
A4	*C. australiensis* Celtidaceae	S.J. Forbes 389	L	H	Australia
7	*C. australis* Celtidaceae	E. Relief 38154	WAG	H	South Africa
8	*C. australis* Celtidaceae	Bochpoderi 11429	WAG	H	Spain (WAG Bot. Gard.)
81	*C. australis* Celtidaceae	Sattarian 22		H	Iran
51	*C. australis* Celtidaceae	A. Sattarian 9		S	Italy (Bot. Gard.)
88	*C. bifidia* Celtidaceae	O. Connar 44	L	H	Madagascar
137	*C. brasiliensis* Celtidaceae	s.n. 145	U	H	South America
33	*C. brasiliensis* Celtidaceae	J. E.Simonis 165	U	H	Paraguay
7	*C. caucasica* Celtidaceae	R. van Velzen 12		S	Uzbekistan
59	*C. edulis* Celtidaceae	M. Chase 20136	L	H	South Korea
3	*C. ehrenbergiana* Celtidaceae	Stephantal 4435	U	H	Mexico
A3	*C. ehrenbergiana* Celtidaceae	H.H. de Leeuw 496	WAG	H	Mexico
6	*C. gomphophylla* Celtidaceae	I. Friis & G. Gilbert 3864	MO, WAG	H	Ethiopia
25	*C. gomphophylla* Celtidaceae	Hafashimana 177	CO	H	Uganda
29, 69	*C. iguanaea* Celtidaceae	M. Nee & K. Taylor 26592	U	H	Mexico
45	*C. jamaicanses* Celtidaceae	G.R. Proctor 2776	U	H	South America
48	*C. julianae* Celtidaceae	Mount Holyoke bot gard		S	Asia
73	*C. koraiensis* Celtidaceae	H.H. de Leeuw 421	WAG	H	Korea (Bot. Gard.)
11	*C. koraiensis* Celtidaceae	R. van Velzen 13		S	Korea (Bot. Gard.)
45	*C. laevigata* Celtidaceae	A. Sattarian 25		S	North America (Bot. Gard.)

Extr. nr	Species	Collection or Gen Bank no.	Herb.	H/S	Origin
1	*C. latifolia* Celtidaceae	Bochpoderi 11429	L	H	Philippines
139	*C. madagascariensis* Celtidaceae	L. Sussman 436A	WAG	H	Madagascar
68	*C. madagascariensis* Celtidaceae	Linda 435A	WAG	H	Madagascar
125	*C. mississippiensis* Celtidaceae	Lumusee 1877	UU	H	North America
77	*C. occidentalis* Celtidaceae	H.H. de Leeuw 504	WAG	H	North America
54	*C. occidentalis* Celtidaceae	H.H. de Leeuw 505	WAG	S	North America (Bot. Gard.)
62	*C. paniculata* Celtidaceae	I.R. Telford 10943	U	H	Malaysia
4	*C. philippensis* Celtidaceae	S.J. Forbes 389	L	H	Australia
78	*C. rhamnifolia* Celtidaceae	S.n. 15	WAG	H	Ethiopia
41	*C. schippii* Celtidaceae	J. Schunke 5989	U	H	Mexico
16, 76	*C. selloviana* Celtidaceae	H.H. de Leeuw 421	WAG	S, H	South America
18, 75	*C. sinensis* Celtidaceae	H.H. de Leeuw 504	WAG	S, H	Japan
44	*C. soyauxii* Celtidaceae	J.-P. Essou 1138	MO	H	Benin
67	*C. tala* Celtidaceae	Meise bot gard		S	South America
59	*C. tessmannii* Celtidaceae	J.J Wieringa 5101	WAG	H	Gabon
50	*C. toka* Celtidaceae	S. Demissew 1709		H	Ethiopia
17	*C. tournefortii* Celtidaceae	H.H. de Leeuw 452	WAG	H	South Europe (Bot. Gard.)
74	*C. tournefortii* Celtidaceae	WAG bot gard 7843		H	Spain (Bot. Gard.)
25	*C. trinervia* Celtidaceae	S.n. 542	U	H	Mexico (U Bot. Gard.)
32	*C. zenkeri* Celtidaceae	C. Donis 1634	MO	H	Congo (Kinshasa)
30	*C. zenkeri* Celtidaceae	S.n. 1768	WAG	H	Cameroon
94	*Chaetachme madagascariensis,* Celtidaceae	G. McPherson 14423	WAG	H	Madagascar
76	*Gironniera hirta* Celtidaceae	R.D. Hoogland 10351	L	H	New Guinea
77	*G. rhamnifolia* Celtidaceae	R.D. Hoogland 10541	L	H	New Guinea
71	*Lozanella trematoides* Celtidaceae	C.G. Pringle, 8983	L	H	South America
65	*Parasponia andersonii* Celtidaceae	J.-Y. Meyer 2556	WAG	H	Polensia

Extr. nr	**Species**	**Collection or Gen Bank no.**	**Herb.**	**H/S**	**Origin**
74	*P. rugosa* Celtidaceae	K. Damas 74501	L	H	New Guinea
12	*Trema micrantha* Celtidaceae	L.W. Chatrou 413	U	H	Bolivia
	Cannabis sativa Cannabaceae	AF500334			
	Humulus lupulus Cannabaceae	AF061992			
	Cecropia sp. Cecropiaceae	AF501615			
	Ampelocera sp. Celtidaceae	AF500335			
	Aphananthe aspera Celtidaceae	AF500352			
	Parasponia tatarinowii Celtidaceae	AF500343			
	Trema africana Celtidaceae	AY488690			
	Brosimum sp. Moraceae	AF500346			
	Ficus sp. *Moraceae*	AF500350			
	Ficus sp., Moraceae	AF500352			
	Morus sp. Moraceae	D86319			
	Ulmus sp. Ulmaceae	AF500337			
	Pellionia sp. Urticaeae	AF500358			

Samenvatting

BIJDRAGE AAN DE BIOSYSTEMATIEK VAN *CELTIS* L. (CELTIDACEAE) MET SPECIALE AANDACHT VOOR DE AFRIKAANSE SOORTEN.

A. SATTARIAN

Celtis L. (Celtidaceae, eerder deel uitmakend van de Ulmaceae) is een genus met voornamelijk boomsoorten, dat van nature is verspreid in Afrika, het Middellandse Zeegebied, Azië, Noord- en Zuid-Amerika, en noordelijk Australië. Buiten het natuurlijke verspreidingsgebied worden diverse soorten in de gematigde zone aangeplant, maar ze komen voor in diverse verschillende ecologische habitats, tropische en gematigde gebieden op alle continenten. Sommige soorten hebben sierwaarde, sommige worden voor hout en herbebossing gebruikt.

Dit proefschrift is gecentreerd op Afrikaanse *Celtis* soorten met de bedoeling een algemene fylogenie van de Celtidaceae te leveren, de verwantschappen van de Afrikaanse soorten te begrijpen, een revisie van de Afrikaanse *Celtis* soorten te maken, de belangrijkste morfologische kenmerken te bestuderen, en een conspectus, een algemeen overzicht van de namen en synoniemen te geven.

Dit onderzoek leverde resultaten, waarvan de volgende zijn uitgelicht: Ulmaceae s.l. zijn niet monofyletisch en wij bevestigen dat de familie in twee delen moet worden opgesplitst: Ulmaceae s.s. en Celtidaceae; de Celtidaceae zouden met de Cannabaceae moeten worden samengevoegd, over het algemeen is *Celtis* zelf monofyletisch, maar voor meer ondersteuning moeten we meer markers gebruiken en soorten toevoegen. In de verwantschap van *Celtis* kunnen een aantal clades worden onderscheiden, speciaal voor de Zuid-Amerikaanse soorten die door de aanwezigheid van doorns in een aparte clade kunnen worden gerangschikt, dit morfologische kenmerk onderscheidt de groep van de rest van het genus *Celtis*. Afrikaanse en Aziatische *Celtis* vormen een gemengde clade, deze kan beïnvloed zijn door de verspreiding (dispersie) van deze soorten.

In totaal zijn er 12 soorten *Celtis* onderscheiden in Afrika en Madagascar: *Celtis adolfi-friderici, C. africana, C. australis, C. mildbraedii, C. gomphophylla, C. prantlii, C. tessmannii, C. toka, C. wightii,* en *C. zenkeri.* Op Madagascar kan men twee endemische soorten aantreffen: *C. bifida* en de onlangs als nieuw beschreven soort *Celtis malagasica*. Voor Australië werd een nieuwe soort afgesplitst uit het "*Celtis philippensis* complex": *Celtis australiensis.* De belangrijkste morfologische kenmerken om soorten te onderscheiden zijn bladvorm, nervatuur, beharing, huidmondjes, bloeiwijzen, stuifmeel, vruchtvorm en die van het endocarp. Twee soorten pollenkorrels konden worden onderscheiden op de basis van hun kiemopening; twee soorten haren zijn te onderscheiden (met en zonder klieren), de huidmondjes vindt men in drie types: paracytisch, cyclocytisch en anisocytisch; de bloeiwijzen zijn bepaald (cymeus) en de vruchten zijn steenvruchten (drupa), het endocarp van *Celtis* varieert van rond-ellipsoïde tot eivormig in verschillende grootte, kleuren en textuur.

De conspectus bevat ongeveer 500 namen op de rangen van soort en infraspecifische taxa, waarvan er vele nog voor publicatie- en typificatie detaillering moeten worden nagezocht. Om betere verwantschapspatronen in *Celtis* te verkrijgen kan in het algemeen worden aanbevolen het genus te revideren voor Azië.

Summary

CONTRIBUTION TO THE BIOSYSTEMATICS OF *CELTIS* L. (CELTIDACEAE) WITH SPECIAL EMPHASIS ON THE AFRICAN SPECIES

A. SATTARIAN

Celtis L. (Celtidaceae, earlier part of the Ulmaceae) is a genus mainly of tree species, which has its natural distribution in Africa, the Mediterranean region, Asia, North and South America, and northern Australia. Outside this natural distribution various species are planted in temperate areas, but they occur in many different ecological habitats, tropical and temperate regions in all continents. Some species are ornamental; some are used for timber and reforestation.

This thesis is focused on African *Celtis* with general objectives such as providing a phylogeny of the Celtidaceae, understanding the relationships of African *Celtis,* preparation of a revision of the African *Celtis* species, a study of the main morphological characters, and a conspectus containing all names and synonyms in the genus.

This thesis provided results, such as: Ulmaceae s.l. is not monophyletic and we confirm that this family has to be split into two families, Ulmaceae s.s. and Celtidaceae; the Celtidaceae should merge with Cannabaceae; in general *Celtis* is monophyletic but for more support we need to add more markers and taxa. In the relationships of *Celtis*, a few clades can be seen especially for South American species, which have thorns and by this morphological character that clade is distinguished from the rest of the genus *Celtis.* African and Asian *Celtis* form a mixed clade, this clade could have been influenced by the dispersal of these species.

In total 12 African *Celtis* are identified in Africa and Madagascar: *Celtis adolfi-friderici, C. africana, C. australis, C. mildbraedii, C. gomphophylla, C. prantlii, C. tessmannii, C. toka, C. wightii,* and *C. zenkeri.* On Madagascar there are two endemic species: *C. bifida* and the newly described species *Celtis malagasica*. For Australia a new species was separated from the "*Celtis philippensis* complex": *Celtis australiensis*. The main morphological characters in African *Celtis* instrumental for the distinction of species include leaf shape, venation, indumentum, stomata, inflorescences, flowers, pollen, fruits and their endocarps. Two pollen types could be distinguished based on the feature of the apertures, also two types of hairs are distinguished (glandular and non-glandular); stomata include three types: paracytic, cyclocytic and anisocytic; inflorescences are cymose and fruit shape are drupes, the endocarp of *Celtis* differs from globose ellipsoid to ovoid with different sizes, colours, and texture.

The conspectus contains about 500 names of specific and infraspecific rank, many of which remain to be verified to complete publication and typification details. Generally for getting better relationship patterns of this genus revision of the Asian *Celtis* is recommended.

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I would like to take this opportunity to express my special thanks to the Biosystematics group, Department of Plant Sciences, Wageningen University, The Netherlands, for providing a congenial atmosphere.

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I appreciate the very useful comments of Dr. R.G. van den Berg, especially for the pollen grain chapter. The discussions with Dr. Ir. F.J. Breteler I consider very instructive.

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Ali. Sattarian, Wageningen 2006.

Curriculum Vitae

Ali Sattarian was born on 19-9-1965 in Tehran, Iran. He graduated from the Daneshmand high school in Tehran city in 1984. In the same year he was accepted as Associate of Science (A.SC.) in the field of Natural Resources (1984-1986). Also in 1986 was accepted as BSc in the Forestry (1986-1989) at the Tehran University. He obtained his Master of Science degree in forestry at the same university (1989-1992). He worked as expert of studying the vegetation in Jihad-e-Sazandege (Center Research) in 1993. He obtained the position of Academic member of Gorgan University (Gonbad-e-Kavooz), where he conducted research and teaching. He was awarded a scholarship to continue his study abroad. He started his Ph.D. at the Biosystematics group in May 2001.
Ali Sattarian is married and has a son, Mohammad Reza, and a daughter, Mobina.

Publications

Sattarian A. & van der Maesen L.J.G. (2005).Two new species of *Celtis* (Celtidaceae) from Australia and Madagascar. Blumea 50: 499-503.

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Summary in Farsi

خلاصه

بیوسیستماتیک درخت داغداغان با تاکید خاص بر قاره افریقا

درخت داغداغان *Celtis spp.* یکی از گونه های درختی متعلق به خانواده Celtidaceae است. این گونه معمولا بصورت درختئ و درکلیه قارها گسترش دارد. جنس مذکور دارای 100گو نه در جهان و پراکنش جغرافیائی این گونه درمناطق معتدله حاره ای ونیمه حاره ای است.,

در شمال قاره افریقا (لیبیِ الجزایرِ مراکش) گونه *Celtis australis* ءِ مناطق ساوانا و حاشیه جنگل ها گونه *Celtis* *C.africana* ، *Celtis toka* ،*مناطق حاره ای* گونه های *Celtis tessmannii, C. adolfi-friderici* ودر مناطق نیمه *حاره ای* گونه های *Celtis prantlii, C. zenkeri , C. mildbraedii* *گسترش یافته است*. این تحقیق در10 فصل خلا صه شده است. درفصل اول نتا یج کلیه تحقیقات انجام شده جمع اوری ومورد تجزیه و تحلیل قرارگرفته واهداف کلی تحقیق تدبین شده است.در فصل دوم وسوم رابطه فیلوژنی (وراثتی) خانواده های Ulmaceae, Celtidaceae ووضعیت های جنسهای انها مورد تحقیق قرار گرفته است. درفصل های چهارم ، پنجم وششم خصوصیات ماکرومورفولوژی و میکرومورفولوژی مورد تحقیق واقع شده است. کلید شناسایی کلیه گونه های مورد مطالعه درفصل هفتم وبحث درمورد گونه های مرکب درفصل هشتم اورده شده است. درفصل نهم کلیه گونه های درخت داغداغان به همراه سایراطاعات مورد نیاز جمع اوری شده است. درفصل دهم خلاصه نتایج ذکرشده است.

اهداف تحقیقات:

- شناسایی و معرفی مهمترین خصوصیات ماکرومورفولوژی (برگ، رگبرگ بندی، گل، میوه) ومیکرومورفولوژی (گرده، روزنه، اندوکارپ میوه) درخت داغداغان.
- شناسایی رابطه فیلوژنی (وراثتی) جنس ، گونه، پراکنش جغرافیائی و مورفولوژی داغداغان.

نتایج تحقیقات:

- شناسای و معرفی دو گونه جدید *Celtis australiensis* Sattarian، *C. malagasica* Sattarian
- مهمترین خصوصیات درشناسایی گونه های این جنس عبارتند از (شکل برگ ، رگبرگ بندی، حاشیه برگ، اندوکارپ میوه).
- معرفی و تهیه کلید شناسایی گونه های مختلف مورد مطا لعه براساس اندوکارپ میوه.
- شناسای و معرفی کلیه گردهای جنس *Celtis* در قاره افریقا
- تهیه کلید شناسایی کلیه گونه های *Celtis* در قاره افریقا
- درمطالعات فیلوژنی (وراثتی) مشخص گردید، خانواده Ulmaceae مونوفلتیک نمی باشد و باید به خانوادهای مختلف تقسیم گردد.
- خانواده Celtidaceae نیز مونوفلتیک نمی باشد و جایگاه جنس های *Celtis, Trema* هنوزکاملا مشخص نیست.
- بطورکلی جنس *Celtis* مونوفلتیک است ولی گونه های افریقا همراه گونه های اسیا دریک گروه clade دیده می شوند.
- ارتباط میان فیلوژنی (وراثتی) وپراکنش جغرافیائی داغداغان در موردگونه های ا مریکای جنوبی صادق است زیرا انها در یک گروه clade قرارمی گیرند.
- میان فیلوژنی ومورفولوژی نیزدراین مطالعات ارتباط معنی داری مشاهده شد ه است، بطوری که گونه های افریقا و اسیا در یک گروه clade قرارگرفته ولحاظ مورفولوژی نیزشبیه یکدیگرمی باشند.

علی ستاریان